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Global Patterns in Community Succession

1. Bryophytes and Forest Decline

By Lee F. Klinger
Department of Geography and Institute of Arctic and Alpine Research, University of Colorado, Boulder

Issue No. 1 in the series:
The Role of Plants in Landscape Transformation

Edited by Paul S. Mankiewicz

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1. Bryophytes and Forest Decline

By Lee F. Klinger
Department of Geography and Institute of Arctic and Alpine Research, University of Colorado, Boulder, 80307*

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The Role of Plants in Landscape Transformation

EDITORS INTRODUCTION

This issue of the memoirs initiates a new series which explores the active role of plants in modifying, regulating, and transforming their surroundings. Individuals, clones, colonies, and communities of plants apparently effect immediate, local, and regional circumstances from square centimeters to hectares. Relations between radiation and temperature, water availability and relative humidity, concentrations of gases and solutes, and microbes and mineral substratum are all apparently affected through the complex properties of plants.

Ecological disturbances have long been recognized as essential processes in ecosystem development. Recent environmental degradation caused by human cultures provides opportunities for ecological restoration and biological remediation which would best be strongly based upon the comparative biology of plants and their cobionts. Our hope is that this series may provide a forum for theoretically informed and empirically grounded discussions of the functional role or niche of plants, encouraging interest and ongoing research in morphology, physiology, systematics, and general organismal plant biology.

Paul S. Mankiewicz, Editor
Memoirs of the Torrey Botanical Club

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ABSTRACT

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Global Patterns in Community Succession: 1. Bryophytes and Forest Decline. Memoirs of the Torrey Botanical Club, Vol. 24, No. 1, 1990.

FOREST DECLINE is now recognized as a global phenomenon affecting forests in both polluted and unpolluted regions, and ranging from the tropics to the subarctic. In light of this, a long-standing hypothesis is re-examined which states that forest decline is primarily an autogenic, successional process whereby, in the absence of large-scale disturbance, mature forests progress toward structurally and compositionally more stable, climax bog communities. A key driving mechanism of this process, called bryophyte-paludification, is the action of ground-dwelling bryophytes which kill very fine feeder roots and impede drainage.

This hypothesis is partially tested in dieback forests of southeast Alaska and northern New York. Root size and health characteristics in surface soils were compared under *Sphagnum* and non-*Sphagnum* sites. Soil water pH was also compared under high *Sphagnum* cover and low *Sphagnum* cover sites in southeast Alaska. Results indicate that the amount of live very fine roots is significantly greater in non-*Sphagnum* sites, and that the relative amount of dead very fine roots is significantly greater in *Sphagnum* sites. Soil water pH is significantly lower in areas of high *Sphagnum* cover compared to low *Sphagnum* cover.

Much testing still must be done before the role of bryophytes in tree mortality can be ascertained, though many of the physiological and ecological patterns associated with paludification are consistent with observations and data reported in the forest decline literature. It is concluded that paludification should be considered as a possible mechanism in global forest decline.

Key words: forest decline, succession, paludification, bryophyte, *Sphagnum*, root mortality, Alaska, New York.

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PREFACE

This paper is the first of a two part series which describes a somewhat novel, more global view of a long-standing, but apparently overlooked, hypothesis of forest decline and community succession, and reports on the results of studies designed to test this hypothesis. The first part focuses on patterns and potential mechanisms of successional change involving bryophyte-tree-soil water interactions. The second part will focus on quantification of various community parameters and environmental factors along a successional sequence from old-growth forest to bog.

The successional viewpoint of this series follows, more-or-less, Clementsian theory, which considers succession to be a deterministic, developmental process of community change directed by communities and landscapes. (The author is fully aware of the more recent, individualistic views which consider succession to be a non-deterministic process controlled primarily by individual–and population–level mechanisms.) The radical nature of this approach is certain to raise the ire of those ecologists who feel that the climax theory of vegetation succession has, after careful examination, been debunked. Their conclusion is based, in part, on the fact that structural and compositional stability has not been found in old-growth forests. Following a literal interpretation of Clementsian climax theory, they are probably right. However, the existence of non-forest climax communities, though often proposed, has never been fully examined. The premise of this series of papers is that bog communities, for the most part, originate from mature forests, and, since bogs exhibit structural and compositional stability on the order of thousands to ten of thousands of years, they merit consideration and examination as climax communities.

INTRODUCTION

High levels of forest decline in industrialized areas of North America and Europe have drawn an intense focus of study on the role of air pollution (including acid precipitation) in tree death. This effort has demonstrated that, although air pollutants may have some effect, they are not the primary causal agents of forest decline (Tamm 1976; Cogbill 1977; Evans 1984; McLaughlin and Bräker 1985; Klein and Perkins 1987; Woodman 1987; Blank *et al.* 1988). Pollution-related injury cannot account for a variety of ecological patterns of tree death. For instance, forest decline with symptomology similar to that found in polluted areas occurs extensively in such unpolluted areas as Alaska (Hennon 1986; Klinger 1988), Hawaii (Hodges *et al.* 1986; Mueller-Dombois 1987), New Zealand (Jane and Green 1983a; Wardle and Allen 1983; Grant 1984), the southern Andes (Veblen *et al.* 1977; Veblen and Lorenz 1987), Borneo (Anderson 1964), and New Guinea (Arentz 1983). These observations suggest the involvement of natural processes of tree death which may be exacerbated by high pollution levels. Most work on possible natural causes of forest decline centers on biotic damaging agents such as insects and fungal pathogens, and on the damaging effects of climate. Little work has been done on community and ecosystem processes related to forest decline, especially with respect to succession (except see Mueller-Dombois 1986). In general, forest decline hypotheses and investigations have tended to be constrained within a rather narrow range of spatial and temporal scales. For instance, there are virtually hundreds of studies on the short-term (≤ 1 year) effects of various pollutants on leaves and branches (and occasionally entire individuals) of trees and crops plants. Yet, few, if any studies address the predicted or observed ecosystem- or global-scale patterns of forest decline occurring presently or over the past few centuries. A more fruitful approach is one which presents and tests a forest decline hypothesis across a wide range of spatial and temporal scales, simultaneously examining systemic, organismic, population, community, landscape, and global patterns and processes of the decline syndrome. This series of papers attempts such a hierarchical approach (*sensu* Allen and Starr 1982) in examining a long-standing, but overlooked, hypothesis of forest decline based on natural mechanisms of vegetation succession which may be significantly affected by air and water pollution.

PATTERNS OF FOREST DECLINE

"Decline" or "dieback" are terms often used synonymously to describe forests where the majority of trees show reduced vigor or are standing dead (Mueller-Dombois 1987). In some forests, obvious causal mechanisms of fire, wind, or flooding, can explain the death of trees. However, in many areas forest dieback cannot be "explained" by these or other mechanisms, although reduced vigor from insects, fungal pathogens, mistletoe, or other forest pests may occur. It is these areas of unexplained forest dieback which are the subject of this paper.

Forest decline is a global phenomenon (Mueller-Dombois 1988) that has been occurring sporadically for at least several hundred years in many, if not most, affected areas (Binns and Redfern 1983; Johnson and Friedland 1986; Kullman 1987; Mueller-Dombois 1987; Hamburg and Cogbill 1988). Forest decline tends to occur in moist to wet sites, though not always (Veblen and Lorenz 1988), and there is growing evidence that tree death can be drought-induced (Johnson *et al.* 1981; Friedland *et al.* 1984; Grant 1984; Vogelmann *et al.* 1985; Jane and Green 1987; Hosking and Hutcheson 1988; Lawesson 1988). Forest dieback is often episodic (Jane and Green 1983b; Franklin *et al.* 1987). In some areas tree death occurs in groups (Anderson 1964; Mueller-Dombois 1987) and it may even exhibit a wave-like progression (Sprugel 1976; Kohyama 1984; Boone *et al.* 1988), but often mortality is random (Binns and Redfern 1983). Forest decline affects mainly mature or old-growth forests, and tends to affect canopy trees more severely than subcanopy trees (Mueller-Dombois 1987). Yet, scattered within heavily-damaged forests are some canopy trees which are barely, if at all, affected (Woodman 1987). Seedling and sapling growth in damaged areas may or may not be strongly inhibited (Mueller-Dombois 1983; Klein and Perkins 1987). Death of surrounding understory has sometimes, but rarely, been observed (Schütt and Cowling 1985).

Affected individuals tend to exhibit dieback beginning at the top (or ends of outer) branches and progressing downward (or inward along the outer branches toward the trunk) (Binns and Redfern 1983; Johnson and Siccama 1983; Mueller-Dombois 1987; Woodman 1987). Decreased diameter growth is commonly associated with forest decline (Cogbill 1977; Johnson *et al.* 1981; Schütt and Cowling

1985; Hinrichsen 1986; Ash 1988). Symptoms of nutrient deficiencies (e.g., chlorosis) and water-stress (e.g., altered water balance) are often present (Klein 1984; Schütt and Cowling 1985; Hinrichsen 1986). In studies where below-ground plant tissue has been examined, mortality of very fine (feeder) roots and mycorrhizae has also been documented (Hawboldt and Skolko 1948; Berry 1955; Toole and Broadfoot 1959; Pomerleau and Lortie 1962; Leaphart and Stage 1971; Bauch 1983; Binns and Redfern 1983; Klein 1984; Schütt and Cowling 1985; Bunyard 1986; Hinrichsen 1986; Jane and Green 1987; Woodman 1987). Of key importance is the observation that feeder root and mycorrhizae mortality occur prior to the onset of aboveground dieback symptoms (Spaulding and MacAloney 1931; Manion 1981; Klein 1984).

FOREST DECLINE HYPOTHESES

The literature abounds in hypotheses of forest decline such that a description of them all is impractical here (see reviews by Manion 1981; Bunyard 1986; Hinrichsen 1986, 1987; Krause *et al.* 1986; Mueller-Dombois 1986; Klein and Perkins 1987, 1988). Instead, overviews and critiques will be presented for the major classes of hypotheses which are currently receiving attention.

Pollution Hypotheses

A large number of hypotheses involve the direct effect of one or more air pollutants, particularly ozone and sulfur dioxide, on foliage or soils (*cf.* Hinrichsen 1986; Prinz *et al.* 1987). Although air pollution almost certainly contributes to forest decline, none of the pollution hypotheses can account for all the observed symptoms of damage (Hinrichsen 1986). Forest decline is extensive in many unpolluted areas of the world, whereas trees in high pollution areas (i.e. metropolitan areas) are largely unaffected. For example, Orange County, California experiences very high pollution levels, and has even received precipitation with a pH as low as 1.69 (Roth *et al.* 1985). Yet, trees and understory vegetation growing in abandoned (non-irrigated and non-fertilized) fields in Orange County exhibit few, if any, signs of stress (*pers. obsv.*). In New England, cloud water acidity and ozone levels were found to be considerably greater at the coast than in the mountains (Kimball *et*

al. 1988), however, higher elevation forests are more heavily affected by dieback in this region. In Norway, no relation was found between air pollution patterns and tree vitality and growth (Tveite 1987). Clearly, some non-pollution mechanism must be involved in the forest decline phenomenon.

- **Multiple Factor Hypotheses**

Another group of hypotheses have evolved in response to the failure of investigators to find a single damaging agent common to all areas of forest decline (McLaughlin and Bräker 1985). These multiple factor hypotheses propose that forest decline is a result of stress induced by the additive effects of several air pollutants on trees and/or soils, which increases the susceptibility of trees to severe climatic conditions, nutrient deficiency, and biotic pathogens (*cf.* Bruck 1985; Schütt and Cowling 1985; Bunyard 1986; Hinrichsen 1986, 1987; Johnson 1987; Klein and Perkins 1987; Matzner and Ulrich 1987; Schulze 1989). Despite their apparently sound ecological underpinnings, these multiple factor hypotheses, like the pollution hypotheses, fail to account for forest decline in areas not significantly influenced by pollution. Furthermore, their high level of complexity renders them very difficult to test, although some success has been made in this regard (Schultze 1989).

- **Natural Decline Hypotheses**

Many studies of forest decline have proposed various natural causal mechanisms including high temperatures (Auclair 1987; Hamburg and Cogbill 1988), low temperatures (Kullman 1987), drought (Hursh and Haasis 1931; Staley 1965; Westing 1966; Leaphart and Stage 1971; Grant 1984; Hosking and Hutcheson 1988), decreased fire frequency (Veblen and Lorenz 1988), severe storms (Shaw 1983; Kanzaki and Yoda 1986), frost (Slatyer 1976), fog (Jane and Green 1987), winter desiccation (Lindsay 1971; Sprugel 1976; Shaw *et al.* 1985; Binns *et al.* 1987), rime-ice (Sprugel 1976), soil degradation (Ugolini and Mann 1979; Walker *et al.* 1983), rising water tables (Isaak *et al.* 1959), receding water tables (Skipworth 1983), browsing animals (Batcheler 1983; Leutert 1988), insect infestations (Busing *et al.* 1988; Sherman and Warren 1988), nematodes (Manion 1981), fungal pathogens (Arentz 1983; Kile 1983; Matson and Boone 1984; Ash 1988; Boone *et al.* 1988),

mycoplasmic organisms (Palzer 1983), and attrition (Marchand *et al.* 1986). Many of these, as well as other studies (e.g., McLaughlin *et al.* 1987), report that two or more natural factors may interact to cause forest decline. In general, these hypotheses have been proposed as explanations for forest decline in specific regions and, individually, do not account for global-scale patterns of forest decline. The idea that they collectively may explain global forest decline is unsatisfactory in that the symptomology of the decline syndrome would be expected to differ significantly from site to site depending upon the primary damaging mechanism(s). The symptoms and patterns of forest decline, such as decline of old-growth forests, dieback from the top down, and high levels of root mortality, are, in fact, remarkably similar throughout the world.

The Decline Disease Hypothesis

The notion that forest dieback results from an interacting set of biotic and abiotic factors is the basis for the decline disease hypothesis (Manion 1981). This hypothesis is similar to the multiple factor hypotheses except that air pollutants may or may not be involved. Specifically, the decline disease hypothesis states that three or more sets of factors are involved in dieback. These are, 1) predisposing factors, those which weaken a plant by imposing permanent stress (e.g., climate, soil moisture, genotype, soil nutrients, and/or air pollutants), 2) incitants, short-term factors which generally cause drastic injury (e.g., insect defoliation, frost, drought, salt, air pollutants, and/or mechanical injury), and 3) contributing factors, organisms which further stress the weakened host (e.g., bark beetles, canker fungi, viruses, and/or root-decay fungi). Tree death, then, results through some combination of factors from all three sets. This hypothesis is testable through site manipulation to control for one or more of the factors associated with decline disease. If tree dieback or death results in the absence of any predisposing or inciting factors, then this hypothesis can be rejected as a cause of a particular decline. The decline-disease hypothesis is a step in the right direction in examining the decline syndrome across a wider scale, but does not go far enough in treating the similarity of decline symptoms across communities and landscapes.

The Cohort Senescence Hypothesis

The cohort senescence hypothesis (Mueller-Dombois 1986)

has recently gained the attention of investigators because it attempts to explain forest decline in an ecological and successional context. The cohort senescence hypothesis postulates that when cohorts (groups of individuals which establish following a large-scale disturbance or dieback) reach old age, their reduced vigor predisposes them to dieback resulting from some "triggering perturbation", thus causing roughly synchronous tree death. The trigger factors may be either biotic or abiotic mechanisms. The common observation of asynchrony in death of cohort stands is explained by invoking differential rates of cohort development, further modified by microsite differences. Although Mueller-Dombois (1987) does not consider pollution-related forest dieback to be a direct consequence of cohort senescence, he does suggest that air pollution may accelerate senescence.

Several investigations have lent support to the cohort senescence hypothesis through findings that dieback was concentrated among mature trees in more-or-less even-aged stands (Sprugel 1976; Stewart and Veblen 1982; Veblen and Stewart 1982; Ward 1982; Jacobi 1983; Lawesson 1988). In fact, Veblen and Stewart (1982) developed a similar, more simple version of the cohort senescence hypothesis independent of Mueller-Dombois' work. They suggest that trees in even-aged stands which establish after catastrophic disturbances may exhibit roughly synchronous death upon reaching old-age. Loehle (1988) proposed an extension of the cohort senescence hypothesis to include the role of tree defenses in explaining patterns of decline.

Other studies have reported findings inconsistent with the cohort senescence hypothesis. Allen and Rose (1983) found that dieback attributed to cohort senescence involved mixed-age stands in New Zealand. In a study of age structure in undisturbed forests of southeast Alaska (that will be further described in Part 2 of this series), dieback was found in all-aged populations in stands dominated by four different tree species (Klinger 1988). A review of ohia (*Metrosideros polymorpha*) forest decline in Hawaii (Hodges *et al.* 1986) concluded that synchronous cohort senescence does not explain the etiology of the decline.

The cohort senescence hypothesis is attractive from several ecological viewpoints. It relates dieback to the developmental stage of dominant forest species, to the successional changes in a forest community following disturbance, to the cyclic nature of population responses after a perturbation,

and to a multitude of modifying influences from biotic and abiotic factors. Still, certain ecological processes such as understory interactions, soil development, and hydrological effects which show non-random relationships to forest decline are not fully considered by this hypothesis. For instance, the ecological role of *Sphagnum* mosses (and other bryophytes), which have been hypothesized as a cause of tree mortality (Lawrence 1958; Banner et al. 1983; Noble *et al.* 1984) and which commonly occur in senescent forest stands in Hawaii (D. Mueller-Dombois, *pers. comm.*) and elsewhere, is not treated in this hypothesis. Neither is the common occurrence of podsolized soils in areas of forest decline (Veblen and Ashton 1982; Veblen and Stewart 1982; Jacobi 1983; Jane and Green 1983a; Walker *et al.* 1983; Hodges *et al.* 1986; Klinger 1988) considered in this hypothesis.

The cohort senescence hypothesis may appear consistent with patterns of death in other organisms such as humans, where a traumatic mechanism causing a physiological failure is much more likely to result in death among the elderly than among more youthful "cohorts". Yet, the ultimate cause of death of any organism is a physiological failure within the organism. Here, then, is a key deficiency of the cohort senescence hypothesis. No physiological mechanism of death is proposed. Until such a mechanism is identified which can account for the full range of dieback symptoms, this hypothesis cannot be fully tested.

Paludification Hypotheses

The term "paludification" was first used by Auer (1928) to refer to the process of establishment and growth of peat-forming plant communities taking place both on dry lands and in bodies of water. In recent years this term has been applied exclusively to the succession from dry land to bog, and the term "terrestrialization" has been applied to the process of bog formation from the infilling of a water body.

Numerous causal mechanisms for paludification have been proposed. Localized paludification is reported to have resulted from various allogenic factors including rising water tables (Isaak *et al.* 1959; Schwintzer 1978; Noble *et al.* 1984), reduced thawing depth (Drury 1956; Viereck 1970), and soil hardpan formation (Ugolini and Mann 1979). Extensive paludification in the British Isles and Scandanavia has been attributed to forest depredation by early humans (Moore 1968, 1975; Iversen 1973).

Paludification has also been attributed to autogenic factors such as impeded drainage through peat formation (Gorham 1957; Allington 1961) and beaver activity (Auer 1930).

Although these mechanisms undoubtedly play an interactive role in paludification, they fail to account for the similarity in spatial and temporal patterns of paludification observed throughout the world. For instance, in all reported cases an abundance of ground-dwelling bryophytes, in most cases *Sphagnum* mosses, occur in or around paludified sites. The above hypotheses implicitly assume that this pattern is an effect of paludification. However, the possibility that bryophytes play a causal role in paludification must be considered.

The Bryophyte-Paludification Hypothesis

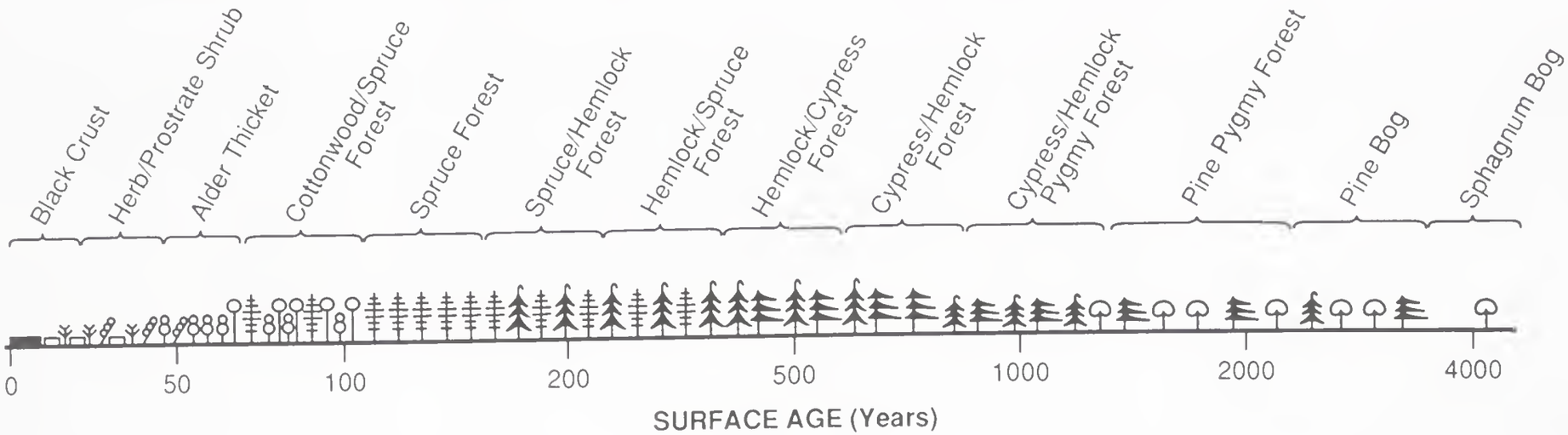
The hypothesis that forest dieback can occur through the spread of ground-dwelling (geophytic) bryophytes which physically and chemically alter the soil, eventually leading to bog formation has been proposed by Weber (1908), Rigg (1917, 1925), Katz (1926), Drury (1956), Lawrence (1958), Heilman (1966), Banner *et al.* (1983), and Noble *et al.* (1984). Several authors have concluded that this paludification process represents one of several successional pathways which converge on climax bog or swamp communities in regions such as Siberia (Katz 1926), southeast Alaska (Zach 1950), northern Alaska (Viereck 1966), British Isles (Walker 1970), and several areas of the tropics (Flenley 1978). Successions from forest to peatland have been described along chronosequences of raised marine beaches and terraces in northern California (Jenny *et al.* 1969), Canada (Glooschenko and Martini 1983), New Zealand (Wardle 1980), and Australia (Walker *et al.* 1983). Antonovsky *et al.* (1987) and Bonan (1988) have successfully modeled paludification in boreal ecosystems by incorporating the effects of geophytic bryophytes in forest dynamics. Klinger and others (1988; Klinger *et al.* 1990) have recently proposed, and tested, a modified version of this 'paludification as succession' hypothesis, called the bryophyte-paludification hypothesis, that emphasizes the importance of autogenic succession (*sensu* Clements 1916) toward bogs, climax vegetation communities which are structurally and compositionally more stable than forests. A central feature of the bryophyte-paludification hypothesis is the recognition that cryptogams, especially geophytic bryophytes (hereafter referred to simply as 'bryophytes' or

'mosses' unless otherwise stated), play key roles in forest dieback, thus driving, in part, the successional process. Unlike other hypotheses of paludification, this modified hypothesis proposes that succession toward climax bog communities is a global process. A schematic example of a generalized successional sequence involving bryophyte-paludification is presented in Figure 1. This is a proposed primary succession from southeast Alaska based mainly on studies by Lawrence (1958), Sprague and Lawrence (1960), Decker (1966), Reiners *et al.* (1971), and Klinger (1988).

The Bryophyte-Paludification Hypothesis in the Context of Successional Theory

Successional theory, which has been developed mainly from a vegetation perspective, is a central topic of debate among ecologists divided, generally, between two viewpoints. The long-standing organismic viewpoint is that succession represents a developmental, ontogenic process in ecosystems (or landscapes), analogous to the maturation process of an organism, which results in the formation of structurally and compositionally stable (climax) communities (Clements 1916; Margalef 1963; Odum 1969). This view holds that succession toward a hypothetical climax community, usually old-growth forest, is a deterministic process of vegetation change in the sense that if one knows the initial environmental and biological conditions the successional sequence can be predicted. Conversely, the more popular individualistic viewpoint considers succession to be an indeterministic process of change which varies according to both the physical environment and the life history traits of the individuals involved (Gleason 1917, 1926). This view questions the existence of climax communities in light of numerous findings that old-growth forests do not exhibit structural or compositional stability (Jones 1945; Raup 1963). Also, early succession has been shown to progress along several different pathways within a given landscape due primarily to the influence of allogenic factors and is therefore not readily predictable (Connell and Slatyer 1977).

The approach taken in this paper, which draws from both of these viewpoints, is that early successional pathways are primarily under the control of allogenic factors and can, therefore, vary widely. However, as succession progresses the increasing importance of autogenic factors causes pathways to ultimately converge onto specific late successional communities, and that, in the absence of large-scale physi-



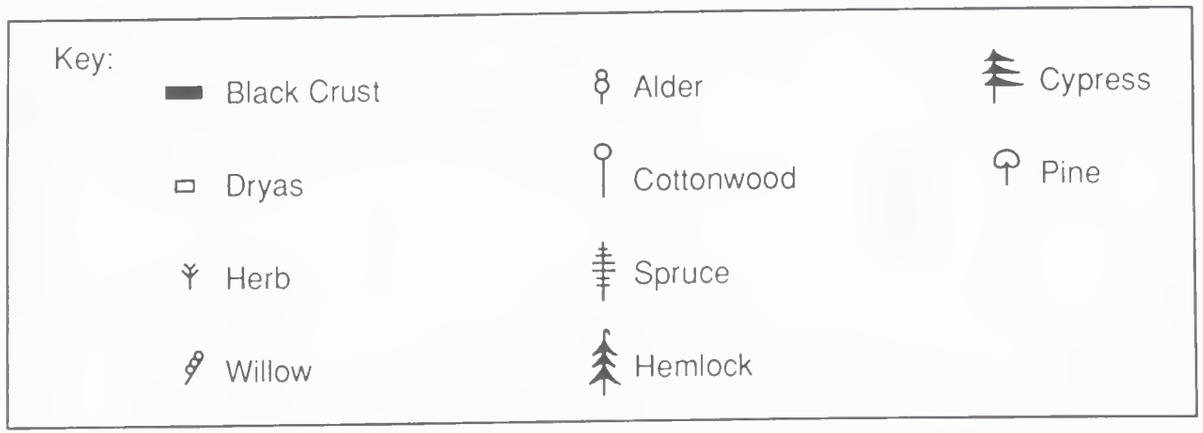


Figure 1.
Schematic depiction of a generalized primary successional sequence involving bryophyte-paludification in southeast Alaska. Based mainly on studies by Lawrence (1958), Sprague and Lawrence (1960), Decker (1966), Reiners *et al.* (1971), and Klinger (1988).

cal disturbance, terrestrial and aquatic vegetation successions converge on bryophyte-dominated communities with organic soils (bogs). Large-scale physical disturbance is defined here as any physical phenomenon resulting in the sudden (≤ 1 yr) decline or death of a majority of the individuals of one or more dominant or sub-dominant taxa in a community. Examples of physical disturbances are fire, landslide, blowdown, flooding, severe drought, heavy dust deposition, and volcanic ashfall. (By this definition of disturbance, arid and semi-arid landscapes are viewed as being continually maintained at relatively early stages of succession due to the frequent occurrence of drought.)

Specific Hypotheses

To better recognize and investigate various spatial and temporal scales involved in bryophyte-paludification, this hypothesis is subdivided into separate hierarchically-related hypotheses:

Hypothesis 1: Bryophytes cause very fine root mortality in surface soils by releasing hydrogen cations and organic acids which deplete nutrient cations and which mobilize aluminum to toxic concentrations.

Hypothesis 2: Tree vigor and growth are reduced through water and nutrient deficiency caused by root mortality.

Hypothesis 3: Tree death results from the direct effects of water and nutrient stress, and/or from the interaction with secondary factors, especially drought, insects, and fungal pathogens.

Hypothesis 4: Bryophyte spread is episodic, resulting in short-term (10^1, 10^2 years) cyclic patterns of forest decline and recovery, although, over the long-term (10^3 years), successional changes toward bog occur.

Hypothesis 5: Bryophytes accelerate podsolization and aid in ironpan formation in iron-rich substrates or claypan formation in aluminum-rich substrates, which results in impeded drainage and soil anaerobicity.

Hypothesis 6: Bryophytes reduce organic matter decomposition rates causing peat accumulation (and higher permafrost tables in cold climates), resulting in impeded drainage and soil

anaerobicity.

Hypothesis 7: Moderate levels of acid precipitation and certain associated pollutants (e.g., nitrates and sulfates) aid in the establishment and growth of most bryophytes.

It is further hypothesized that epiphytic bryophytes, lichens, and perhaps other cryptogams play an important, but as yet undetermined, role in forest decline. This hypothesis is slightly elaborated from the original version (Klinger 1988) particularly in its emphasis on the role of aluminum in root mortality.

The bryophyte-paludification hypothesis differs from other hypotheses of forest decline in that, 1) it proposes a related set of causal factors (bryophytes) that appear to be common to all areas of forest decline, 2) it postulates that forest dieback is a mechanism of progressive successional change toward more stable bog communities, 3) it considers the interactive effects of vegetation communities, atmosphere, soils, and groundwater in forest decline, and 4) it is organized in a hierarchical fashion to encompass the full range of spatial and temporal scales of forest decline. A graphic depiction of the hierarchical organization of the paludification hypothesis is presented in Figure 2. In this figure the hypothesized effects of bryophyte interactions on soils and vegetation during succession are listed according to the temporal and spatial scales at which they occur, more-or-less, continuously.

It should be emphasized that this hypothesis does not attribute all dieback to a single causal factor. There are perhaps thousands of different species of bryophytes and other cryptogams which may have the ability, each in a somewhat different way, to impose a strong modifying influence on the surrounding plants and soil. Microclimatic and soil changes during community succession, along with increased levels of air pollutants in certain regions, may exacerbate forest decline. In fact, this hypothesis allows for the full set of interacting, multiple factors associated with tree death to operate in conjunction with (or may even be considered mechanisms of) successional change.

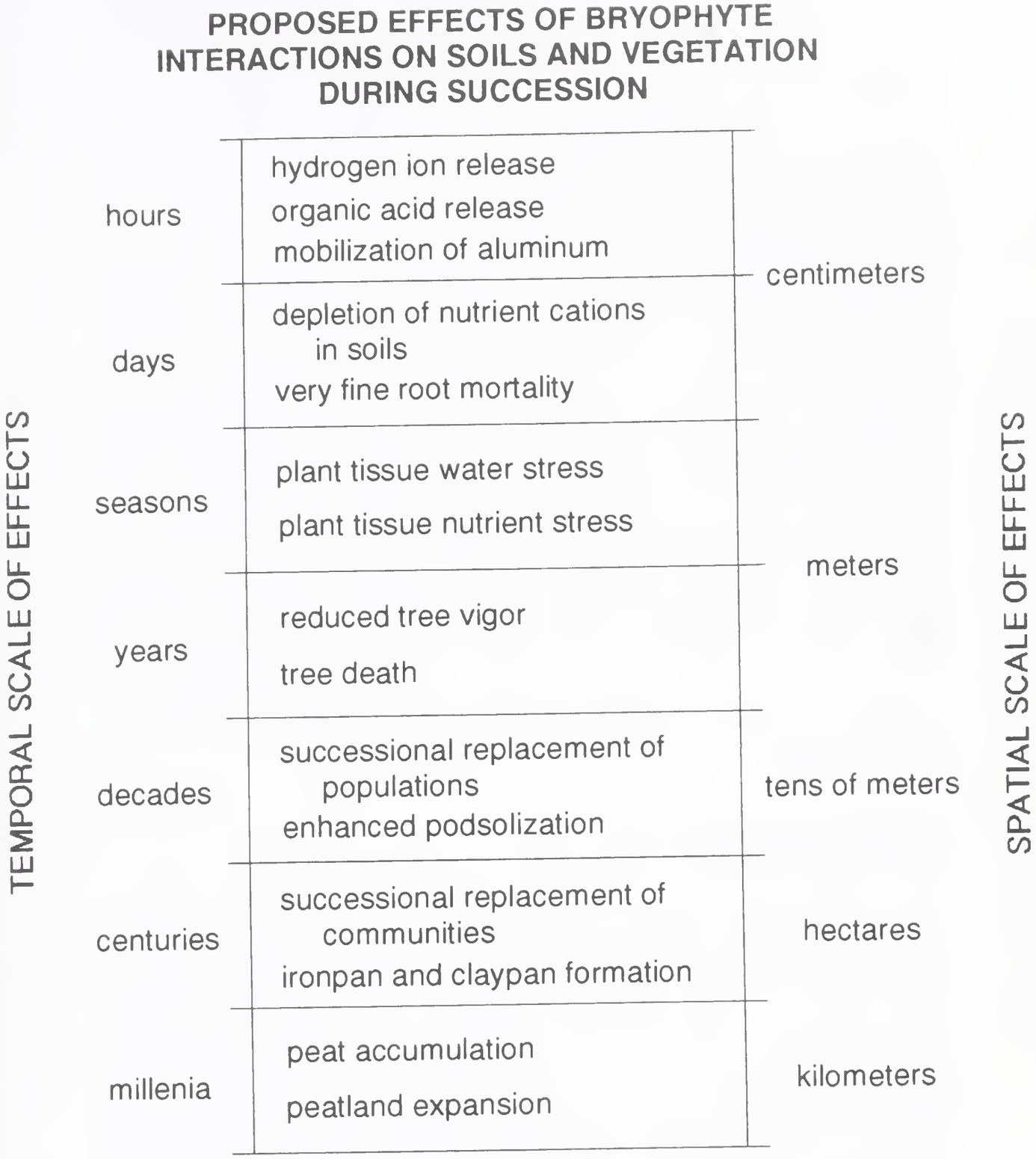


Figure 2.
Proposed successional processes of soil and vegetation change affected by bryophyte dynamics. Processes are arranged hierarchically according to the temporal and spatial scales at which they operate, more-or-less, continuously.

OBJECTIVES

This study is designed as a partial test of the bryophyte-paludification hypothesis. Predictions were made of patterns in root structure and hydrologic pH, based on *Hypothesis 1*, in relation to one group of bryophytes (*Sphagnum* spp.). The objectives were to investigate whether observed patterns in declining old-growth forests support the following predicted patterns: 1) live biomass of the very fine surficial roots should be less under *Sphagnum* mats than under forest litter, 2) the dead/(dead+live) ratio of very fine surficial root biomass should be greater under *Sphagnum* mats than under forest litter, and 3) areas of high *Sphagnum* cover should exhibit lower pH of soil water compared to areas of low *Sphagnum* cover. Predictions 1 and 2 are based on the assumption that *Sphagnum* mosses directly affect only the actively absorbing feeder (very fine) roots. Prediction 1 also assumes that *Sphagnum* moss mats have not persisted at the sites long enough to significantly affect live root biomass patterns among the larger diameter roots due to the effect of decreased recruitment to the larger diameter root classes. The other hypotheses (*2-7*) are not tested in this paper but are treated here in a discussion of findings from other studies. Part 2 of this series will present results of tests and more detailed discussion of *Hypotheses 4-6*.

STUDY AREAS

Root samples and hydrologic pH measurements were taken from dieback forests on Kruzof Island, Alaska during the summer of 1986. Root samples were also taken from dieback forests on Whiteface Mountain, New York during the summer of 1987. The sampling site on Kruzof Island (57°05' N; 135°45' W) was located 5 km inland on an east-facing hillside (slopes ranging between 0° and 15°) at 210-m elevation (Figure 3). Weather records from nearby Sitka, Alaska (15 km east) indicate a mean annual temperature of 6°C and a mean annual precipitation of 226 cm. The site is an old-growth, all-aged (median tree age – 210 yrs.; maximum tree age – 589 yrs.) forest dominated by western hemlock (*Tsuga heterophylla* [Bong.] Sarg.), mountain hemlock (*T. mertensiana* [Bong.] Sarg.), and Alaska cypress (*Chamaecyparis nootkatensis* [Lamb.] Spach) with lesser

amounts of Sitka spruce (*Picea sitchensis* [Bong.] Carr.), and an understory dominated by bryophytes and ericaceous shrubs. Soils are tentatively classified as typic cryohumods and cryic placohumods (Soil Survey Staff 1975; Klinger 1988). The geological substrate is the Mt. Edgecumbe ash, an andesitic pyroclastic deposit dated at about 9000 BP (Klinger *et al.* 1989).

The Whiteface Mountain site (44°22' N; 73°54' W) is located at 1320-m elevation on a northwest-facing slope (slopes range between 0° and 15°) (Figure 4). Mean annual temperature is 2°C and mean annual precipitation is about 125 cm (Sprugel 1976). The site, in a "fir dieback wave" (Sprugel 1976), is a roughly even-aged forest (mean tree age – 55 yrs.) dominated by balsam fir (*Abies balsamea* [L.] Mill.) with small amounts of paper birch (*Betula papyrifera* Marsh). The understory is dominated by bryophytes and pteridophytes (ferns). There is no evidence of past forest fire, logging, or other large-scale physical disturbance at the site. Soils are tentatively classified as lithic cryorthods and lithic cryohumods (*cf.* Reiners and Lang 1979). The geological substrate is the Whiteface Mountain anorthosite, a crystalline plutonic rock dominated by plagioclase feldspar (Sprugel 1976).

METHODS

Root Biomass Analysis

Soil cores were collected from Kruzof Island in August of 1986 and from Whiteface Mountain in July of 1987. On Kruzof Island, ten pairs of 500-cc cores (10,000 cc total), and on Whiteface Mountain, five pairs of cores (5000 cc total) were taken from the root zone, the upper 10 cm of the soil mostly comprised of organic (O) horizons. Twenty random soil cores taken from the same site on Kruzof Island in 1985 indicated that 82% of the root biomass occurred in this zone (Klinger, unpublished data), a pattern which has been noted in other old-growth forests (Havas and Kubin 1983). For both sites, each pair consisted of a sample from under a mat of *Sphagnum* (100% cover of *Sphagnum* spp., mostly *Sphagnum girgensohnii* Russow) and the other from under forest litter, located within two meters of each other and equidistant from the nearest trees. The forest litter sites had a 10–20% cover of assorted feathermosses (mainly *Hylocomnium splendens* [Hedw.] B.S.G.). The *Sphagnum*

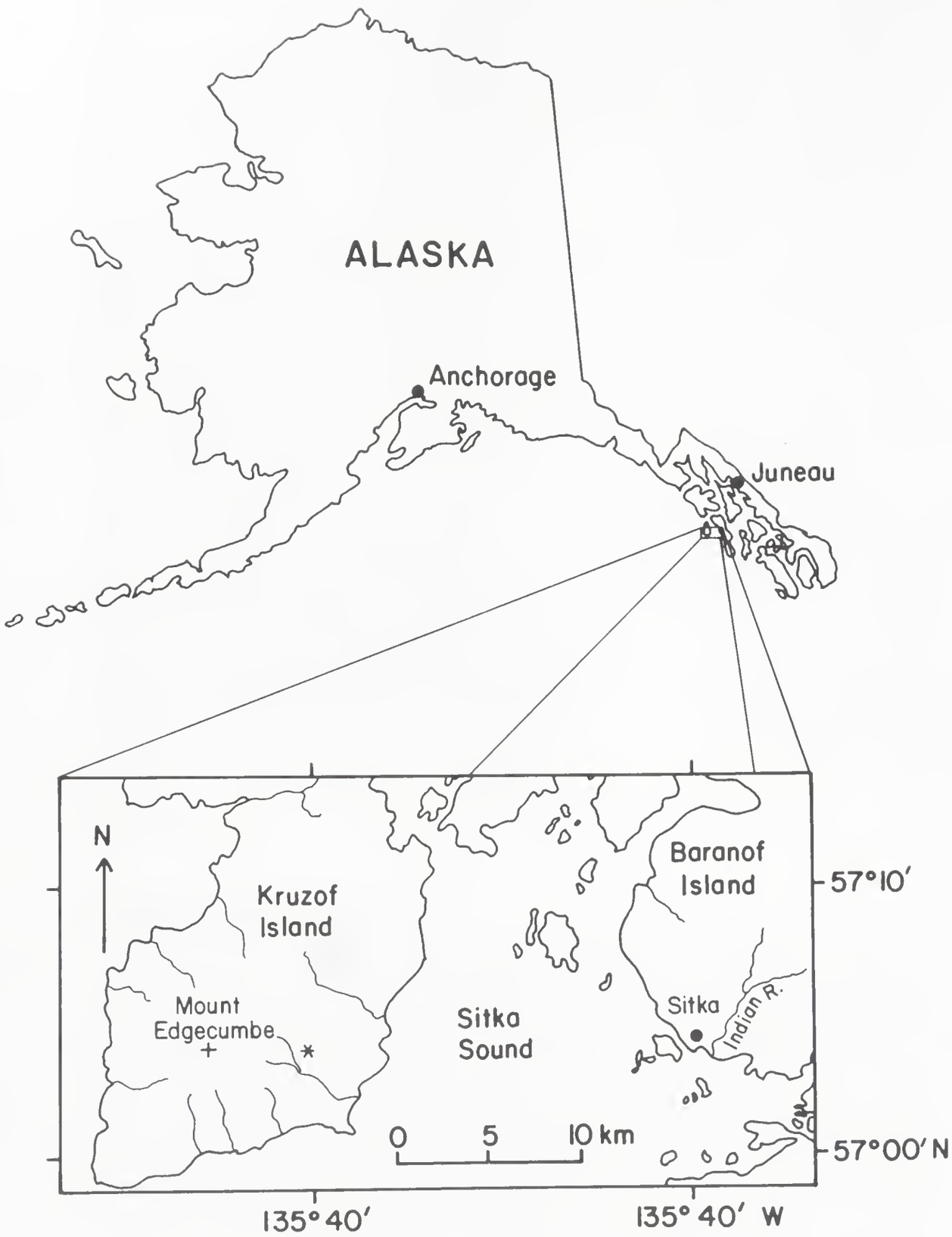


Figure 3.
Location map of the Kruzof Island region, Alaska. The Kruzof Island sampling site is starred.

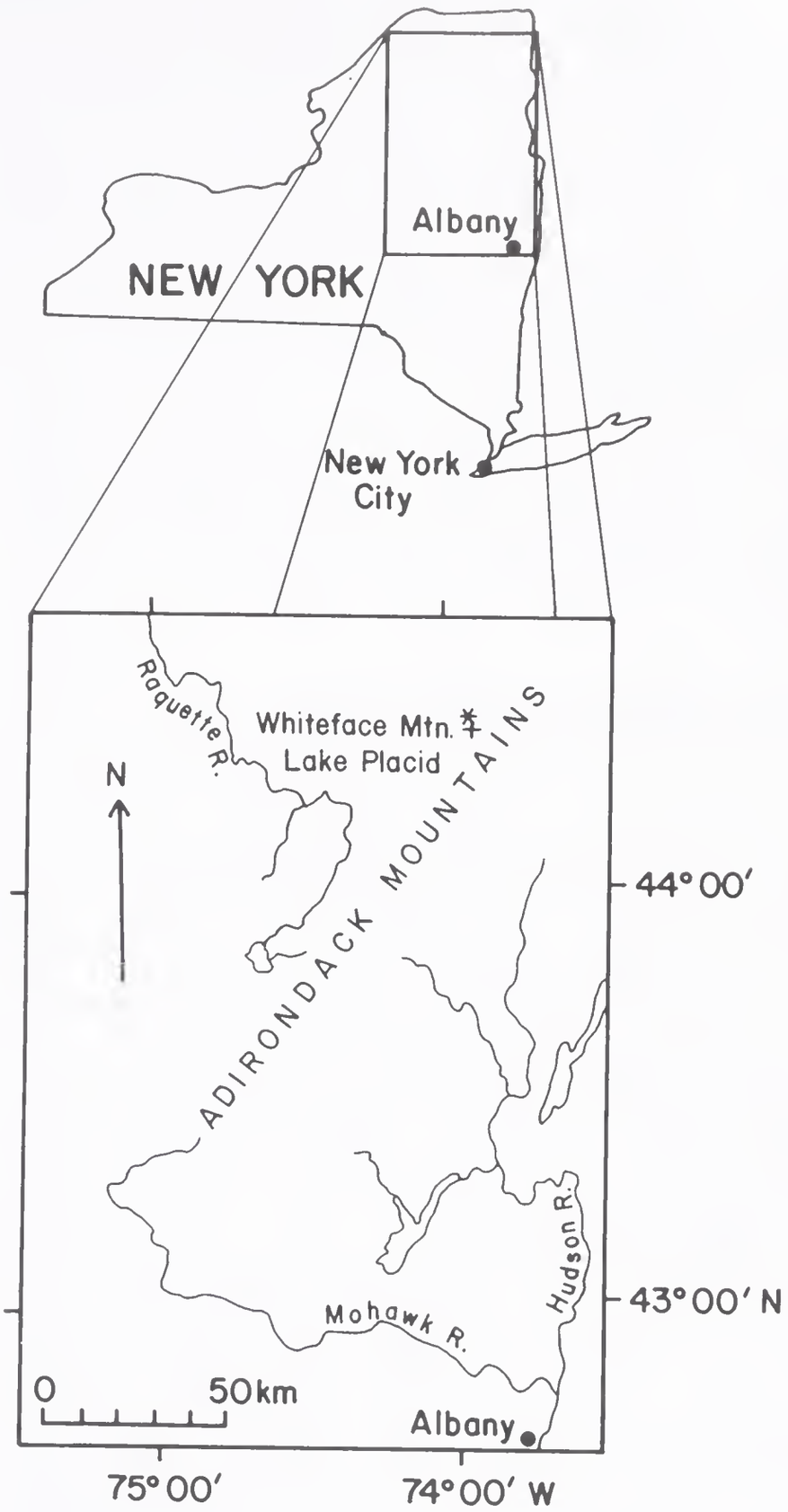


Figure 4.
Location map of the Adirondack Mountain region, New York. Whiteface Mountain sampling site is starred.

mats at the Whiteface Mountain site were notably thicker (10 to 20 cm) than those at the Kruzof Island site (5 to 10 cm). Samples were bagged in plastic and kept refrigerated until analyzed.

In the lab, samples were washed successively through 2.00-. 0.991-, and 0.833-mm soil sieves (U.S. standard sieve sizes 10, 18, and 20, respectively) (*cf.* Smith and Klinger 1985). Roots were then sorted into live and dead components (*cf.* Dennis and Johnson 1970) according to the following diameter classes: <1 mm (very fine), 1-2 mm (fine), 2-5 mm (medium), and >5 mm (coarse). Although both woody and herbaceous roots were analyzed together, the vast majority of root tissue (estimated at over 95%) was woody. Samples were then dried at 100°C for 24 hours and weighed. Values for all components were converted to mg/cc.

Throughfall and Soil Water pH

The pH of throughfall and of soil water at 10-cm, 30-cm and 60-cm depths was measured on Kruzof Island daily from August 1 to August 19, 1986 (19 days with recorded rainfall). Daily throughfall measurements are from two locations at each of two sites, one site in an area of high *Sphagnum* cover dominated by Alaska cypress with mountain hemlock as a sub-dominant, and the other site in an area of low *Sphagnum* cover dominated by mountain hemlock with Alaska cypress and Sitka spruce as sub-dominants. Daily soil water measurements are from two lysimeters at each of the three depths located at each of the two sites (high and low *Sphagnum* cover) (12 lysimeters total). Throughfall was collected in teflon rain gauges mounted 50 cm above the soil surface. Soil water was collected by suction (6.0×10^4 Pa) through ceramic-bottom soil lysimeters. Plasticware was thoroughly rinsed with distilled water, followed by a rinse in the solution to be measured. Measurements of pH were taken in a shelter at the monitoring site immediately after collection. Temperature-corrected determinations to the nearest tenth of a pH unit were made with a field pH meter and combination electrode, using a standard two-point calibration with fresh buffer solutions (pH 4.00 and 7.00). The accuracy of the pH meter was verified using a dilute NADP/NTN standard solution with a pH of 4.30 ± 0.1 and a conductance of 22 (± 2) $\times 10^{-6}$ $S \cdot m^{-1}$.

RESULTS AND INTERPRETATION

The results of paired comparisons *t*-tests (Sokal and Rohlf 1981) performed on the root biomass data are presented in Tables 1 (Alaska) and 2 (New York). Table 1 indicates significantly greater live root biomass of the very fine, fine, coarse, and total root fractions in non-*Sphagnum* sites compared to *Sphagnum* sites in the Alaska study area. Dead root mass of the very fine fraction is significantly greater under *Sphagnum* mats. More importantly, the dead/(dead+live) root ratio of the very fine root fraction is significantly greater under *Sphagnum* mats.

Table 2 indicates similar root biomass trends occur in the New York study area, however the absolute biomass values are consistently less than in the Alaska study area. Significantly greater live root biomass of the very fine and total root fractions occurs in non-*Sphagnum* compared to *Sphagnum* sites. There are no significant differences observed in the dead root fractions, however, the dead/(dead+live) root ratio of the very fine root biomass is significantly greater under *Sphagnum* mats.

The overall results indicate significantly less live root mass, especially in the very fine (feeder) root fraction, under *Sphagnum* sites. This pattern may be the result of decreased root productivity and/or increased root mortality under *Sphagnum* sites compared to non-*Sphagnum* sites. If increased root mortality is involved, then increased absolute and relative amounts of dead very fine roots should be observed. Dead very fine root biomass tends to be greater under *Sphagnum* mats, however, this trend is significant only in the Alaska study area. There are highly significant differences in the dead/(dead+live) ratio of very fine root biomass in both study areas. These differences could be attributable either to increased rates of very fine root mortality or to decreased decomposition rates under *Sphagnum* mats. Decreased decomposition rates, though possibly having some effect, cannot account for these results for two reasons, 1) the effects of decreased decomposition should be observed in all root fractions, not solely the fine root fraction as the data indicate, and 2) decreased decomposition does not account for the significant trends among live root biomass. On the whole, increased levels of root mortality under *Sphagnum* mats appears to be the best explanation for these results, although decreased root production under *Sphagnum* mats may be partly involved.

Table 1. Average dry weight (± std.err.) of live and dead roots and average values for dead/(dead+live) root ration by diameter class in surface soils of *Sphagnum* and non-*Sphagnum* sites (n=20) on Kruzof Island, Alaska. The *t*-values are based on paired comparisons, the probabilities are two-tailed.

	Sphagnum	non-*Sphagnum*	*t*-value
	Live Roots[1]		
very fine [2]	1.91 ± 0.28	2.93 ± 0.48	2.67 *[3]
fine	0.74 ± 0.12	1.66 ± 0.27	3.28 **
medium	1.08 ± 0.26	1.89 ± 0.36	2.15
coarse	0.58 ± 0.32	5.66 ± 2.02	2.66 *
total	4.32 ± 0.63	12.14 ± 2.23	3.95 **
	Dead Roots		
very fine	0.84 ± 0.15	0.15 ± 0.04	4.77 ***
fine	0.40 ± 0.11	0.32 ± 0.11	0.67
medium	0.34 ± 0.17	0.18 ± 0.09	1.30
coarse	0.03 ± 0.02	0.22 ± 0.16	1.22
total	1.60 ± 0.88	0.88 ± 0.17	2.28 *
	Dead/(Dead+Live)		
very fine	0.31 ± 0.04	0.05 ± 0.01	6.01 ***
fine	0.35 ± 0.08	0.15 ± 0.02	2.33 *
medium	0.22 ± 0.08	0.08 ± 0.04	1.58
coarse	0.06 ± 0.05	<0.01	1.29
total	0.28 ± 0.04	0.08 ± 0.01	4.38 **

1. units in mg • cm^3
2. diameter classes: very fine, <1 mm; fine, 1–2 mm; medium, 2–5 mm; coarse, >5 mm
3. significance levels: * , p≤.05; **, p≤.01; ***, p≤.001

Table 2. Average dry weight (± std.err.) of live and dead roots and average values for dead/(dead+live) root ration by diameter class in surface soils of *Sphagnum* and non-*Sphagnum* sites (n=20) on Whiteface Mountain, New York. The *t*-values are based on paired comparisons, the probabilities are two-tailed.

	Sphagnum	non-*Sphagnum*	*t*-value
	Live Roots[1]		
very fine [2]	0.68 ± 0.16	2.26 ± 0.26	9.96 ***[3]
fine	0.90 ± 0.27	0.89 ± 0.20	0.06
medium	0.65 ± 0.27	0.90 ± 0.28	0.72
coarse	0.07 ± 0.07	1.22 ± 0.63	1.97
total	2.29 ± 0.44	5.27 ± 0.72	3.80 *
	Dead Roots		
very fine	0.66 ± 0.24	0.24 ± 0.05	1.45
fine	0.10 ± 0.03	0.20 ± 0.09	1.45
medium	0.10 ± 0.04	0.25 ± 0.17	1.03
coarse	0	0	----
total	0.86 ± 0.26	0.69 ± 0.25	0.44
	Dead/(Dead+Live)		
very fine	0.46 ± 0.05	0.10 ±0.03	4.79 **
fine	0.10 ± 0.03	0.18 ± 0.06	1.46
medium	0.17 ± 0.10	0.21 ± 0.14	0.22
coarse	----	----	----
total	0.29 ± 0.08	0.12 ± 0.41	1.67

1. units in mg • cm^3
2. diameter classes: very fine, <1 mm; fine, 1–2 mm; medium , 2–5 mm; coarse, >5 mm
3. significance levels: * , p≤.05; **, p≤.01; ***, p≤.001

The results for the live very fine root fraction support prediction 1. However, as is indicated by the data from the Alaska study site, some of the larger live root fractions also show some significant differences between *Sphagnum* and non-*Sphagnum* sites. This is possibly the result of an incorrect assumption that *Sphagnum* mats are short-lived. If the mats persist for several years, then a lower biomass of the larger root fraction may be observed, not necessarily from mortality of larger roots, but from the effects of decreased recruitment from the very fine root fraction. The trends in the dead/(dead+live) very fine root fraction in both study areas are consistent with prediction 2.

So far as is known by the author, these are the first data reporting a direct correlation between bryophytes and spatial patterns in live and dead root biomass. Although it does not establish a cause-and-effect relationship, this correlation is a prerequisite step for further testing of the hypothesis that bryophytes cause root mortality. An alternative explanation for these data is that the opening of the forest canopy due to dieback has increased light levels to the forest floor, thus stimulating the growth of *Sphagnum* mosses. The presence of *Sphagnum* mosses may, therefore, be an effect rather than a cause of the decline. Although this alternative hypothesis cannot be ruled out, there is evidence to suggest it is unlikely. First, it would seem rather improbable that canopy opening due to dieback would allow *Sphagnum* mosses to invade only those sites with high root mortality, as the data suggest. Although site moisture might be expected to increase locally where root mortality occurs, *Sphagnum* establishment is almost certainly not limited by moisture availability considering the very high and nearly constant precipitation found in the Alaskan site. Secondly, this hypothesis would require that non-random root mortality occurs at, coincidently, the same spatial and temporal scales exhibited by *Sphagnum* mat expansion.

Throughfall and soil water pH results of the Alaska study area are presented in Figure 5 along with paired comparisons *t*-test results comparing high *Sphagnum* cover vs. low *Sphagnum* cover sites. The analyses indicate that throughfall pH in the high *Sphagnum* cover site (4.59) is significantly greater than in the low *Sphagnum* cover site (4.23). These differences are undoubtedly related to differences in forest composition described above. The important point concerning throughfall is that water entering the soil at the low *Sphagnum* cover site is significantly more acidic than at the

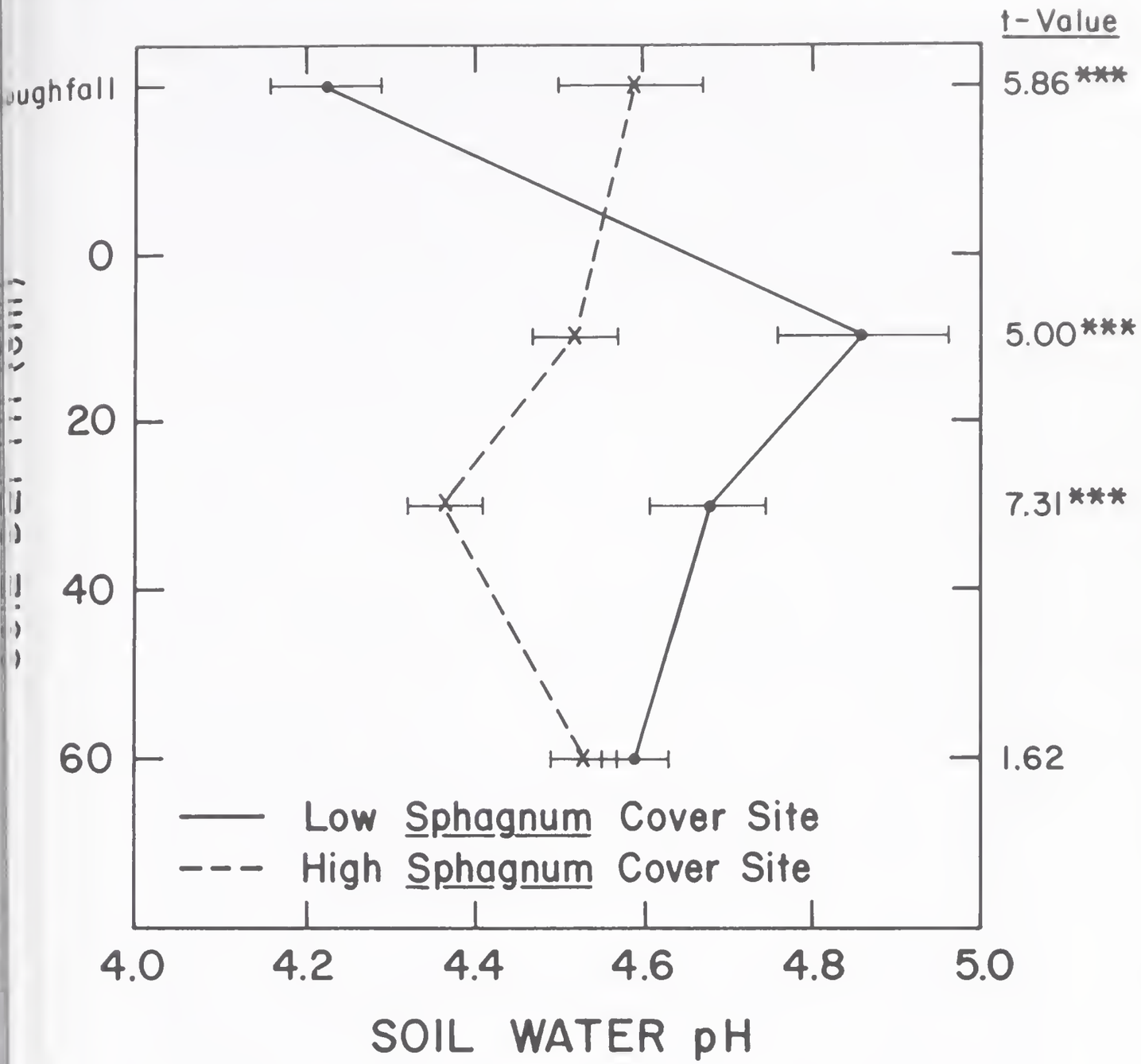


Figure 5.
Average pH values and standard error bars of throughfall and soil water for sites with high *Sphagnum* cover (dashed line) and low *Sphagnum* cover (solid line) in dieback forests on Kruzof Island, Alaska. The *t*-values are based on paired comparisons of high vs. low *Sphagnum* cover sites (df = 18).

high *Sphagnum* cover site. Conversely, soil water pH is significantly more acidic at the 10-cm depth in the high *Sphagnum* cover site (4.52) compared to the low *Sphagnum* cover site (4.86). Thus, the net effect of high *Sphagnum* cover on infiltrating water is the lowering of pH by .07 units, whereas the pH of infiltrating water in the low *Sphagnum* cover site increased by .63 units. A similar trend between the high and low *Sphagnum* cover sites is observed at the 30-cm depth, except that pH values (4.36 and 4.68, respectively) are lower than at the 10-cm depth. At the 60-cm depth soil water pH is essentially identical for both sites.

These results indicate that *Sphagnum* mosses are associated with a significantly lower soil water pH in the surface and near-surface soils in the Alaskan study area. This finding is consistent with the predicted trend (prediction 3). This finding could be explained either by the direct acidification of the soil water by *Sphagnum* mosses, or by a soil pH dependent growth pattern of *Sphagnum* mosses. However, the observation that, on smooth ground surfaces in and around the study area, *Sphagnum* mats expand radially in a near circular fashion to diameters of several meters or more (which is the scale of significant variation in soil water pH measured here) suggests that the soil pH's in the study area do not present a barrier to the invasion of *Sphagnum* mosses. Direct acidification of surrounding water by live *Sphagnum* mosses and by *Sphagnum* peat has been well-documented in laboratory studies (Skene 1915; Baas-Becking and Nicolai 1934; Clymo 1963). Clearly, the best explanation for these results is the direct acidification of the soil water by *Sphagnum* mosses.

Taken together these data are fully consistent with the hypothesis that acidification due to bryophytes, in this case *Sphagnum* mosses, depletes nutrients cations and mobilizes aluminum causing very fine root mortality. However, without data on nutrient cation and aluminum concentrations in soil water, the exact mechanism by which mosses may kill roots cannot be determined. Nutrient deprivation of tree roots through interception by mosses may be one contributing mechanism in root mortality (Strong and La Roi 1983). It may even be that bryophytes are releasing allelopathic chemicals that have yet to be identified. *Sphagnum* mosses can strongly modify surface hydrology through absorptive and conductive mechanisms which operate at the community level (Hayward and Clymo 1982; Mankiewicz 1987),

thus creating anaerobic conditions in surface soils lasting several days or even weeks during and after periods of rainfall and snowmelt. Very fine root mortality, therefore, may be due to the lack of oxygen and/or to the toxic effects of hydrogen sulfide which forms in reduced soils (Lees 1973; Armstrong 1975). Indeed, many herbaceous, shrub, and tree species associated with *Sphagnum* possess aerenchyme in their roots (Sjörs 1950; Coutts and Philipson 1978) presumably to prevent oxygen deficiency. Regardless of the exact mechanisms of root mortality, if bryophytes are responsible, then larger scale patterns and processes of forest decline associated with bryophytes will be evident.

DISCUSSION

The importance of these results is that correlations exist between root biomass, soil water pH, and *Sphagnum* cover in areas of dead and dying trees, and that plausible mechanisms of interaction between these factors exist which can account for observed patterns of tree death and forest decline. Considering that root dynamics play a key role in forest decline, and that bryophytes, especially *Sphagnum* spp., are common in areas of forest dieback, the root-bryophyte relationship needs to be carefully studied.

Bryophyte-Root-Soil Interactions

Excessive very fine root mortality has been documented in other sites where *Sphagnum* mosses are present (Armstrong and Boatman 1967; Hennon 1986; Hodges *et al.* 1986; Jane and Green 1987). In addition, the release of hydrogen cations and especially the production of organic acids, such as fulvic acid, by both live and dead bryophyte tissue could readily increase the amount of soluble aluminum in soil water (James and Riha 1984; Tyler *et al.* 1987). Fine root mortality in areas of forest decline is related to soil acidification (Matzner and Ulrich 1987) and to high levels of aluminum in soils (Ulrich *et al.* 1980; Klein 1984; Hodges *et al.* 1986), especially where calcium levels are low (Hoyle 1971; Matzner *et al.* 1986). Aluminum appears to act antagonistically with calcium, inhibiting calcium uptake which results in tissue damage in the root tips (Hüttermann and Ulrich 1984). Higher aluminum contents were found in fine roots of declining sugar maple trees compared to healthy trees (McLaughlin *et al.* 1987). Soluble aluminum concentrations

are reported to be high in organic soil horizons (1.4 $mmol \cdot kg^{-1}$ [James and Riha 1984]; 1.2 $mmol \cdot kg^{-1}$ [Joslin *et al.* 1988]) and in seepage water (10 to 20 $mg \cdot L^{-1}$ [Matzner and Ulrich 1987]) under declining forests. In a laboratory experiment, Joslin and Wolfe (1989) reported a significant negative correlation between soil aluminum (up to concentrations of about 1.2 $mmol \cdot kg^{-1}$) and the live root biomass of oaks. Besides the direct toxic effect on roots, it has been suggested that high levels of aluminum in the soil may also interfere with calcium and magnesium uptake and transport in plants (Matzner and Ulrich 1987; Joslin *et al.* 1988), thus slowing cambial growth and weakening trees (Shortle and Smith 1988). Acidification and high concentrations of aluminum and other metal ions in soil water are also known to repress the growth of several species of mycorrhizal fungi (Klein 1984).

Root mortality causes decreased water and nutrient uptake, resulting in symptoms of water and nutrient deficiency. Catastrophic xylem dysfunction in woody plants appears to be brought about by water stress (Tyree and Sperry 1988). Tree parts highest and farthest from the ground should be most affected by xylem dysfunction, while lower parts receiving enough water may show no ill effects (Tyree *et al.* 1987). Thus, taller (and generally larger) trees should be more affected by root mortality than shorter ones. Chlorosis of leaves and other nutrient deficiency symptoms should be evident at some stage of dieback. Decreased radial growth of trees should also be evident.

Effects of Acid Deposition on Bryophytes

As indicated in several studies, a moderate amount of acid deposition may favor the establishment and spread of bryophytes. Gorham *et al.* (1987) have suggested that in weakly acid peatlands with low alkalinity, acid deposition is likely to promote the invasion of *Sphagnum* mosses. Field studies have shown notable increases, nearly 100%, in *Sphagnum* moss growth in peatlands that were experimentally acidified with moderate amounts (400 to 500 $\mu Eq \cdot L^{-1} \cdot yr^{-1}$) of nitrate and sulfate (Bayley *et al.* 1987; Rochefort 1987; Rochefort and Vitt 1988). However, in a laboratory study Ferguson and Lee (1979) found that sulfate at (feasible atmospheric) concentrations of up to 8 mM has no effect upon photosynthesis of *Sphagnum*. It is relevant to note here the findings that enhanced growth of *Sphagnum* in lakes is associated with lake acidification in

the eastern United States (Hendrey and Vertucci 1980; Wile *et al.* 1985) and in Sweden (Grahn 1977; Hultberg and Grahn 1976). Studies on the effects of acid deposition on other bryophytes (e.g., *Pleurozium schreberi* [Brid.] Mitt., *Tomenthypnum nitens* [Hedw.] Loeske) indicate, in general, that acidity in the pH range of 3.5 to 5.6 stimulates their growth, particularly if nitrates are abundant (Hutchinson *et al.* 1986, 1987; Raeymaekers and Glime 1986; Rochefort 1987; Rochefort and Vitt 1988). Conversely, these and other studies (Austin and Wieder 1987; Clymo 1987; Lee *et al.* 1987) indicate that acid deposition containing higher levels of nitrate and sulfate appear to be detrimental to the growth of *Sphagnum* and other bryophytes.

One study of particular relevance reports as much as 50 to 80% reduction in bryophyte cover over a 14-year period attributed to acid rain in dieback forests on Camels Hump, Vermont (Klein and Bliss 1984). Experimental manipulations of one species of bryophyte (*Polytrichum ohioense* Ren. & Card.) led the authors to conclude that metal ions in acid rain may be the cause of bryophyte decline. The conclusions of the Klein and Bliss (1984) study contradict the findings and ideas presented in this paper, so their work requires a careful examination.

Klein and Bliss (1984) base their results of bryophyte cover on estimates apparently made by different investigators in the two periods of sampling (1965 and 1979). Subjective coverage estimates between investigators are known to vary significantly, and cannot be reliably used to test for changes in plant cover. Their objective determinations of bryophyte frequency (i.e. the number of plots in which bryophytes were present) are reliable and, ironically, indicate that in eight of the eleven sites, the number of plots containing bryophytes was greater in 1979 than in 1965. Their experiment showed growth decline of *Polytrichum ohioense* in media of increasing hydrochloric acid concentrations. However, acid precipitation is comprised primarily of nitric and sulfuric acids which, as previously discussed, stimulate bryophyte growth at moderate concentrations. Finally, it is puzzling that *Sphagnum* mosses are not reported in their study. Observations on Camels Hump during July of 1987 indicate that *Sphagnum* mosses are abundant in the upper elevation dieback forests (northern coniferous zone) (*pers. obsv.*). Either *Sphagnum* mosses have spread rapidly over the intervening years, or they were somehow missed in the earlier sampling schemes. In light

of the present data on root mortality in relation to *Sphagnum* mosses, a careful evaluation of temporal and spatial patterns of *Sphagnum* on Camels Hump should be undertaken before any conclusions on the effects of acid rain on bryophyte cover are made there.

Symptoms and Patterns of Forest Decline Related to Paludification

The ecophysiology of *Sphagnum* mosses, especially their preference for and production of acidic conditions, is similar to other bryophyte taxa (e.g. *Polytrichum* spp., *Aulacomnium* spp., *Dicranum* spp.). If acidification and resultant aluminum mobilization are the primary mechanisms of root death, then other bryophytes could be involved in forest decline. In recent reconnaissances, by the author, of over 100 locations of forest dieback spanning North America, bryophyte cover was observed to be extensive at all sites, and most often included large mats of *Sphagnum* and/or *Polytrichum* species. Conversely, nearby healthy forests exhibited little or no bryophyte cover. In West Germany, mosses and forest dieback have been observed to go "hand in hand" (B. Ulrich, *pers. comm.*). Forest dieback in sites containing *Sphagnum* and other bryophytes has been reported for Alaska (Drury 1956; Hennon 1986), Canada (Auer 1928, 1930; Allington 1961; Sjörs 1963; Foster 1984), central United States (Waterman 1926; Potzger 1934; Conway 1949; Isaak *et al.* 1959; Heinselman 1963, 1970; Buell and Buell 1975; Schwintzer 1978), eastern United States (Rigg and Strausbaugh 1949; Paratley and Fahey 1986; Stephenson and Adams 1986), southern United States (Buell and Cain 1943; Harcombe and Marks 1983), British Isles (McVean 1964), Scandinavia (Malmer 1965; Reinikainen *et al.* 1984), Siberia (Katz 1926), Hawaii (Hodges *et al.* 1986), New Zealand (Veblen and Stewart 1982; Jane and Green 1987), Australia (Millington 1954), New Guinea (Flenley 1978), and Chile (Alhonen and Auer 1979; Veblen and Ashton 1982). Unfortunately, none of these studies was designed to examine the role of bryophytes in forest decline. The intention of reporting these observations and studies of the co-occurrence of bryophytes and forest decline is not to present evidence for a cause-and-effect relationship, but rather to point out that a potentially important ecological pattern exists that has previously gone unreported in overviews of forest decline.

Furthermore, in any initial presentation of a possible cause-and-effect relationship, it is prudent to first assess whether the cause and the effect are spatially related. If even one of these forest declines did not contain bryophytes, then a strong bit of evidence would exist against the bryophyte-paludification hypothesis.

Community and ecosystem patterns of forest decline are fully consistent with bryophyte-caused root mortality. As has been reported, fine root mortality precedes the onset of aboveground dieback symptoms. Taller trees should be more susceptible to dieback because of the large water demands and root pressures necessitated by the height to which water must be forced in the xylem. However, where bryophyte cover is thick and continuous even seedlings and saplings may be affected. Trees that are water stressed, but surviving, may be suddenly damaged or killed by a drought. Water and nutrient stressed trees are more susceptible to damage by secondary agents such as frost, insects, fungal pathogens, and perhaps air pollution. Dieback forest should also be more prone to treefall, windthrow, and landslide disturbances because of the loss of anchorage and soil cohesion associated with root mortality. Since bryophytes and tree roots are not uniformly distributed, healthy trees may exist along side dead or dying trees. Tree death also occurs in groups, which may be delimited by clusters of moss mats centered, for instance, in topographic lows. *Sphagnum* mosses have been observed to aggregate into radially expanding "waves", which on slopes tend to progress uphill due to the damming of surficial water by the uphill margin of the moss mat creating favorable microsites for growth. In forested areas, *Sphagnum* wave propagation may be further enhanced by the greater accumulation of blowing snow transported from the more exposed dieback areas upwind of the wave. *Sphagnum* mosses appear to favor sites with late-lying snow (pers. obs.). Episodes of forest decline may be related either to episodic drought or to the observed episodic nature of bryophyte growth (Conway 1948; Aaby 1976; Berglund 1983). The cause of episodic bryophyte growth is unknown, though it may be related to cyclic variations in community dynamics or climate (Aaby 1976).

Old-growth forest of moist and wet environments which show the greatest incidence of dieback also possess a very high bryophyte cover. Early successional forests, which are rarely affected by dieback, have little or no bryophyte cover.

The rarity of severe forest dieback in and around heavily-polluted metropolitan areas may be due both to the tendency for these forests to be early successional, as well as to the negative effects of high levels of acid precipitation on bryophytes.

The symptoms and patterns reported above are based on forest decline studies from around the world, including both high- and low-elevation forests in tropical, subtropical, temperate, and boreal regions. For this reason, and since bogs and swamps occur in virtually every region of the world, it is proposed that bryophyte-paludification is global in nature.

CONCLUSION

Although evidence presented here supports the bryophyte-paludification hypothesis of forest dieback, the hypothesis remains mostly untested. Considerable information on bryophyte and root ecophysiology, heavy metal and humic acids in the soil, and community dynamics of forests will be required for several dieback areas in order to more fully evaluate the hypothesis. Interspecific differences among bryophytes in their effects on trees and soils should be examined. Since bryophytes are opportunists, their seasonal growth patterns and rates also need to be studied.

The ideas presented here do not imply that all tree death is attributable to paludification mechanisms. Clearly tree death can involve damaging agents that act synchronously (e.g., insects, mistletoe) or even singly (e.g., Dutch elm disease) in the absence of bryophytes. However, in forest diebacks for which no clear causal factors have been identified, paludification mechanisms could be operative and should be examined. This hypothesis has an advantage over many other hypotheses on forest decline in that it can be readily tested. In fact, simple observation can reject this hypothesis on the grounds that if bryophytes are not found in areas of active, unexplained forest dieback, then they cannot be involved in tree mortality.

Whatever the cause of forest decline, natural mechanisms of tree death must be characterized in order to fully evaluate the role of pollution and other human effects. Ecosystem and landscape-level patterns deserve particular attention if one hopes to develop a theory of forest decline around a conceptual framework of successional theory.

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REFERENCES

Aaby, B. 1976. Cyclic climatic variations in climate over the past 5,500 years reflected in raised bogs. Nature 263:281-284.

Allen, R.B. and A.B. Rose. 1983. Regeneration of southern rata (*Metrosideros umbellata*) and kamahi (*Weinmannia racemosa*) in areas of dieback. Pac. Sci. 37:433-442.

Allington, K.R. 1961. The bogs of central Labrador-Ungava: an examination of their physical characteristics. Geografiska Annaler 43:401-417.

Alhonen, P. and V. Auer. 1979. Stratigraphy of peat deposits in Tierra del Fuego, South America: a review of the results of Finnish expeditions. In: Classification of Peat and Peatland. International Symposium in Hyytiala, Finland, pp. 273-281.

Allen, T.F.H. and T.B. Starr. 1982. Hierarchy: Perspectives for Ecological Complexity. The University of Chicago Press, Chicago.

Anderson, J.A.R. 1964. The structure and development of the peat swamps of Sarawak and Brunei. The Journal of Tropical Geography 18:7-16.

Antonovsky, M.Ya., F.Z. Glebov, and M.D. Korzukin. 1987. A regional model of long-term wetland-forest dynamics. International Institute for Applied Systems Analysis, Paper No. WP-87-63.

Arentz, F. 1983. Nothofagus dieback on Mt. Giluwe, Papua, New Guinea. Pac. Sci. 37:453-458.

Armstrong, W. 1975. Waterlogged soils. In: J.R. Etherington (ed.), Environment and Plant Ecology. Wiley, New York, pp. 181-218

Armstrong, W. and D.J. Boatman. 1967. Some field observations relating the growth of bog plants to conditions of soil aeration. J. Ecol. 55:101-110.

Ash, J. 1988. Nothofagus (Fagaceae) forest on Mt. Giluwe, New Guinea. New Zealand J. Bot. 26:245-258.

Auclair, A.N.D. 1987. The climate change theory of forest decline. Proceedings of the IUFRO Conference on

Woody Plant Growth in a Changing Physical and Chemical Environment, July 27-30, Vancouver. University of British Columbia Press, Vancouver.

AUER, V. 1928. Some future problems of peat bog investigations in Canada. Commentations Forestales 1:1-31.

AUER, V. 1930. Peat bogs in southeastern Canada. Can. Dept. Mines, Geol. Surv. Mem. 162:1-32.

AUSTIN, K.A. AND R.K. WIEDER. 1987. Effects of elevated H^+, SO_4^{2-}, NO_{3-}, and NH_4^+ in simulated acid precipitation on the growth and chlorophyll content of 3 North American *Sphagnum* species. The Bryologist 90:221-229.

BAAS-BECKING, L.G.M. AND E. NICOLAI. 1934. The ecology of a sphagnum bog. Blumea 1:10-44.

BANNER, A., J. POJAR, AND G.E. ROUSE. 1983. Postglacial paleoecology and successional relationships of a bog woodland near Prince Rupert, British Columbia. Can. J. For. Res. 13:938-947.

BATCHELER, C.L. 1983. The possum and rata-kamahi dieback in New Zealand: a review. Pac. Sci. 37:415-426.

BAUCH, J. 1983. Biological alterations in the stem and root of fir and spruce due to pollution influence. In: B. Ulrich & J. Pankrath (eds.), Effects of Accumulation of Air Pollutants in Forest Ecosystems. D. Reidel Pub. Co., Dordrecht, pp. 377-386.

BAYLEY, S.E., D.H. VITT, R.W. NEWBURY, K.G. BEATY, R. BEHR, AND C. MILLER. 1987. Experimental acidification of a *Sphagnum*-dominated peatland: first year results. Can. J. Fish. Aquat. Sci. 44:194-205.

BERGLUND, B.E. 1983. Palaeoclimatic changes in Scandinavia and on Greenland – tentative correlation based on lake and bog stratigraphical studies. Quat. Stud. in Poland 4:27-44.

BERRY, F.H. 1955. Investigations of possible causes of sweetgum blight. Plant Dis. Reptr. 39:270-272.

BINNS, W.D., AND D.B. REDFERN. 1983. Acid rain and forest decline in West Germany. Forest Commission

Research and Development Paper 131, Edinburgh, Scotland.

Binns, W.D., D.B. Redfern, and K. Rennolls. 1987. Forest decline – the view from Britain. In: T.C. Hutchinson & K.M. Meema (eds.), Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems. Springer-Verlag, Berlin, pp. 69-81.

Blank, L.W., T.M. Roberts, and R.A. Skeffington. 1988. New perspectives on forest decline. Nature 336:27-30.

Bonan, G.B. 1988. A simulation model of environmental processes and vegetation patterns in boreal forests: test case Fairbanks, Alaska. International Institute for Applied Systems Analysis, Paper No. WP-88-63.

Boone, R.D., P. Sollins, and K. Cromack, Jr. 1988. Stand and soil changes along a mountain hemlock death and regrowth sequence. Ecology 69:714-722.

Bruck, R.I. 1985. Boreal montane ecosystem decline in the southern Appalachian mountains: potential role of anthropogenic pollution. Air Pollutants Effects on Forest Ecosystems, Conference Proceedings. St. Paul, May 8-9, pp. 137-155.

Buell, M.F. and H.F. Buell. 1975. Moat bogs in the Itasca Park area, MN. Bull. Torrey Bot. Cl. 102:6-9.

Buell, M.F. and R.L. Cain. 1943. The successional role of southern white cedar, *Chamaecyparis thyoides*, in southeastern North Carolina. Ecology 24:85-93.

Bunyard, P. 1986. The death of the trees. The Ecologist 16:4-13.

Busing, R.T., E.E.C. Clebsch, C.C. Eagar, and E. F. Pauley. 1988. Two decades of change in a Great Smoky Mountains spruce-fir forest. Bull. Torrey Bot. Cl. 115:25-31.

Clements, F.E. 1916. Plant Succession: An Analysis of the Development of Vegetation. Carnegie Institution of Washington, Publ. 242.

Clymo, R.S. 1963. Ion exchange in *Sphagnum* and its relation to bog ecology. Annals of Botany 27:309-324.

CLYMO, R.S. 1987. Interactions of *Sphagnum* with water and air. In: T.C. Hutchinson & K.M. Meema (eds.), Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems. Springer-Verlag, Berlin, pp. 513-529.

COGBILL, C.V. 1977, The effect of acid precipitation on tree growth in eastern North America. Water, Air, and Soil Pollution 8:89-93.

CONNELL, J.H. AND R.O. SLATYER. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. The American Naturalist 111:1119-1144.

CONWAY, V.M. 1948. Von Post's work on climatic rhythms. New Phytol. 47:220-237.

CONWAY, V.M. 1949. The bogs of central Minnesota. Ecol. Monogr. 19:173-205.

COUTTS, M.P. AND J.J. PHILIPSON. 1978. The tolerance of tree roots to waterlogging. II. Adaptation of Sitka spruce and Lodgepole pine to waterlogged soil. New Phytol. 80:71-77.

DECKER, H.F. 1966. Plants. In: A. Mirsky (ed.), Soil Development and Ecological Succession in a Deglaciated Area of Muir Inlet, Southeast Alaska. Institute of Polar Studies Report No. 20, Ohio State University, Columbus, pp. 73-95.

DENNIS, J.G. AND P.L. JOHNSON. 1970. Shoot and rhizome-root standing crops of tundra vegetation at Barrow, Alaska. Arct. Alp. Res. 2:253-266.

DRURY, W.H., JR. 1956. Bog flats and physiographic processes in the upper Kuskokwim River region, Alaska. In: R.C. Rollins & R.C. Foster (eds.), Contributions from the Gray Herbarium of Harvard University. No. 178. The Gray Herbarium of Harvard University, Cambridge, pp. 1-127.

EVANS, L.S. 1984. Botanical aspects of acidic precipitation. Bot. Rev. 50:449-491.

FERGUSON, P. AND J.A. LEE. 1979. The effects of bisulfate and sulfate upon photosynthesis in *Sphagnum*. New Phytol. 82:703-712.

FLENLEY, J.R. 1978. The Equatorial Rain Forest: A Geological History. Butterworths, London.

FOSTER, D.R. 1984. The dynamics of *Sphagnum* in forest and peatland communities in southeastern Labrador, Canada. Arctic 37:133-140.

FRANKLIN, J.F., H.H. SHUGART, AND M.E. HARMON. 1987. Tree death as an ecological process. BioScience 37:550-556.

FRIEDLAND, A.J., R.A. GREGORY, L. KARENLAMPI, AND A.H. JOHNSON. 1984. Winter damage to foliage as a factor in red spruce decline. Can. J. For. Res. 14:963-965.

GLEASON, H.A. 1917. The structure and development of the plant association. Bulletin of the Torrey Botanical Club 44:463-481.

GLEASON, H.A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club 53:7-26.

GLOOSCHENKO, W.A. AND I.P. MARTINI. 1983. Wetlands of the Attawapiskat River mouth, James Bay, Ontario, Canada. Wetlands 3:64-76.

GORHAM, E. 1957. The development of peatland. Quart. Rev. Biol. 32:145-166.

GORHAM, E., J.A. JANSSENS, G.A. WHEELER, AND P.H. GLASER 1987. The natural and anthropogenic acidification of peatlands. In: T.C. Hutchinson & K.M. Meema (eds.), Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems. Springer-Verlag, Berlin, pp. 493-512.

GRAHN, O. 1977. Macrophyte succession in Swedish lakes caused by deposition of airborne acid substances. Water, Air, and Soil Pollution 7:295-306.

GRANT, P.J. 1984. Drought effect on high-altitude forests, Ruahine Range, North Island, New Zealand. New Zealand J. Bot. 22:15-28.

HAMBURG, S.P. AND C.V. COGBILL. 1988. Historical decline of red spruce populations and climatic warming. Nature 331:428-431.

HAYWARD, P.M. AND R.S. CLYMO. 1982. Profiles of water content and pore size in *Sphagnum* and peat, and their relation to peat bog ecology. Proc. R. Soc. Lond., Ser. B, 215:299-325.

HARCOMBE, P.A. AND P.L. MARKS. 1983. Five years of tree death in a Fagus-Magnolia forest, southeast Texas (USA). Oecologia 57:49-54.

HAVAS, P. AND E. KUBIN. 1983. Structure, growth and organic matter content in the vegetation cover of an old spruce forest in northern Finland. Ann. Bot. Fennici 20:115-149.

HAWBOLDT, L.S. AND A.J. SKOLKO. 1948. Investigation of yellow birch dieback in Nova Scotia in 1947. J. For. 46: 659-671.

HEILMAN, P.E. 1966. Change in distribution and availability of nitrogen with forest succession on north slopes in interior Alaska. Ecology 47:825-831.

HEINSELMAN, M.L. 1963. Forest sites, bog processes, and peatland types in the glacial Lake Agassiz region, Minnesota. Ecol. Monogr. 33:327-274.

HEINSELMAN, M.L. 1970. Landscape evolution, peatland types, and the environment in the Lake Agassiz Peatlands Natural Areas, Minnesota. Ecol. Monogr. 40:235-261.

HENDREY, G.R. AND F. VERTUCCI. 1980. Benthic plant communities in acidic Lake Colden, New York: *Sphagnum* and algal mat. In: D. Drablos and A. Tollan (eds.), Proc., Int. Conf. Ecol. Impact of Acid Precip. SNSF Project, Oslo, pp. 314-315.

HENNON, P.E. 1986. Pathological and ecological aspects of decline and mortality of *Chamaecyparis nootkatensis* in southeast Alaska. Doctoral dissertation, Oregon State University, Corvallis.

HINRICHSEN, D. 1986. Multiple pollutants and forest decline. Ambio 15:258-265.

HINRICHSEN, D. 1987. The forest decline enigma. BioScience 37:542-546.

HODGES, C.S., K.T. ADEE, J.D. STEIN, H.B. WOOD, AND R.D. DOTY. 1986. Decline of Ohia (*Metrosideros polymor-*

pha) in Hawaii: a review. USDA Forest Service General Technical Report PSW-86.

HOSKING, G.P. AND J.A. HUTCHESON. 1988. Mountain beech (*Nothofagus solandri* var. *cliffortioides*) decline in the Kaweka Range, North Island, New Zealand. New Zealand J. Bot. 26:393-400.

HOYLE, M.C. 1971. Effect of the chemical environment on yellow birch root development and top growth. Plant and Soil 35:623-633.

HULTBERG, H. AND O. GRAHN. 1976. Effects of acid precipitation on macrophytes in oligotrophic Swedish lakes. J. Great Lakes Res. 2:208-217.

HURSH, C.R. AND F.W. HAASIS. 1931. Effects of 1925 summer drought on southern Appalachian hardwoods. Ecology 12:380-386.

HUTCHINSON, T.C., M. DIXON, AND M. SCOTT. 1986. The effect of simulated acid rain on feather mosses and lichens of the boreal forest. Water, Air and Soil Pollution 31:409-416.

HUTCHINSON, T.C., M. SCOTT, C. SOTO, AND M. DIXON. 1987. The effect of simulated acid rain on boreal forest floor feather moss and lichen species. In: T.C. Hutchinson & K.M. Meema (eds.), Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems. Springer-Verlag, Berlin, pp. 411-426.

HUTTERMANN, A. AND B. ULRICH. 1984. Solid phase-solution-root interactions in soils subjected to acid deposition. Phil. Trans. R. Soc. Lond. B 305:353-368.

ISAAK, D., W.H. MARSHALL, AND M.F. BUELL. 1959. A record of reverse plant succession in a Tamarack bog. Ecology 40: 317-320.

IVERSEN, J. 1973. The Development of Denmark's Nature Since the Last Glacial. Geological Survey of Denmark, V Series, No. 7-C.

JACOBI, J.D. 1983. Metrosideros dieback in Hawaii: a comparison of adjacent dieback and non-dieback rain forest stands. New Zealand J. Ecol. 6:79-97.

JAMES, B.R. AND S.J. RIHA. 1984. Soluble aluminum in acidified organic horizons of forest soils. Can. J. Soil Sci.

64:637-646.

JANE, G.T. AND T.G.A. GREEN. 1983a. Vegetation mortality in the Kaimai ranges, North Island, New Zealand. Pac. Sci. 37:385-389.

JANE, G.T. AND T.G.A. GREEN. 1983b. Episodic forest mortality in the Kaimai Ranges, North Island, New Zealand. New Zealand J. Bot. 21:21-31.

JANE, G.T. AND T.G.A. GREEN. 1987. Etiology of forest dieback areas within the Kaimai Range, North Island, New Zealand. New Zealand J. Bot. 24:513-527.

JENNY, H., R.J. ARKLEY, AND A.M. SCHULTZ. 1969. The pygmy forest-podsol ecosystem and its dune associates of the Mendocino coast. Madroño 20:60-75.

JOHNSON, A.H. 1987. Deterioration of red spruce in the northern Appalachian mountains. In: T.C. Hutchinson & K.M. Meema (eds.), Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems. Springer-Verlag, Berlin, pp. 333-345.

JOHNSON, A.H. AND A.H. FRIEDLAND. 1986. Recent and historic red spruce mortality: evidence of climatic influence. Water, Air, and Soil Pollution 30:319-330.

JOHNSON, A.H., T.G. SICCAMA, D. WANG, R.S. TURNER, AND T.H. BARRINGER. 1981. Recent changes in patterns of tree growth rate in the New Jersey pinelands: a possible effect of acid rain. J. Environ. Qual. 10:427-430.

JOHNSON, A.H. AND T.G. SICCAMA. 1983. Acid deposition and forest decline. Environ. Sci. Technol. 17:294A-305A.

JONES, E.W. 1945. The structure and reproduction of the virgin forest of the north temperate zone. The New Phytologist 44:130-148.

JOSLIN, J.D., J.M. KELLY, M.W. WOLFE, AND L.E. RUSTAD. 1988. Elemental patterns in roots and foliage of mature spruce across a gradient of soil aluminum. Water, Air and Soil Pollution 40:375-390.

JOSLIN, J.D. AND M.H. WOLFE. 1989. Aluminum effects on northern red oak seedling growth in six forest soil horizons. Soil Sci. Soc. Am. J. 53:274-281.

KANZAKI, M. AND K. YODA. 1986. Regeneration in subalpine coniferous forests II. Mortality and the pattern of death of canopy trees. The Botanical Magazine 99:37-52.

KATZ, N.S 1926. *Sphagnum* bogs of central Russia: phytosociology, ecology, and succession. J. Ecol. 14:177-202.

KILE, G.A. 1983. Armillaria root rot in eucalypt forests: aggravated endemic disease. Pac. Sci. 37:459-464.

KIMBALL, K.D., R. JAGELS, G.A. GORDON, K.C. WEATHERS, AND J. CARLISLE. 1988. Differences between New England coastal fog and mountain cloud water chemistry. Water, Air and Soil Pollution 39:383-393.

KLEIN, R.M. 1984. Effect of acidity and metal ions on water movement through red spruce. In: D.D. Adams & W.P. Page (eds.), Acid Deposition. Plenum Press, New York, pp. 303-322.

KLEIN, R.M. AND M. BLISS. 1984. Decline in surface coverage by mosses on Camels Hump Mountain, Vermont: possible relationship to acidic deposition. The Bryologist 87:128-131.

KLEIN, R.M. AND T.D. PERKINS. 1987. Cascades of causes and effects of forest decline. Ambio 16:86-93.

KLEIN, R.M. AND T.D. PERKINS. 1988. Primary and secondary causes and consequences of contemporary forest decline. The Botanical Review 54:1-43.

KLINGER, L.F. 1988. Successional change in vegetation and soils of southeast Alaska. Doctoral dissertation, University of Colorado, Boulder.

KLINGER, L.F., S.A. ELIAS, V.M. BEHAN-PELLETIER, AND N.E. WILLIAMS. 1990. The bog climax hypothesis: fossil arthropod and stratigraphic evidence in peat sections from southeast Alaska. Holarctic Ecology 13:72–80.

KOHYAMA, T. 1984. Regeneration and coexistence of two Abies species dominating subalpine forests in central Japan. Oecologia 62:156-161.

KRAUSE, G.H.M., U. ARNDT, C.J. BRANDT, J. BUCHER, G. KENK, AND E. MATZNER. 1986. Forest decline in Europe:

development and possible causes. Water, Air and Soil Pollution 31:647-668.

KULLMAN, L. 1987. Little Ice Age decline of a cold marginal *Pinus sylvestris* forest in the Swedish Scandes. New Phytologist 106:89-122.

LAWRENCE, D.B. 1958. Glaciers and vegetation in southeastern Alaska. Am. Sci. 46:89-122.

LAWESSON, J.E. 1988. Stand-level dieback and regeneration of forests in the Galapagos Islands. Vegetatio 77:87-93.

LEAPHART, C.D. AND A.R. STAGE. 1971. Climate: a factor in the origin of the pole blight disease of Pinus monticola Dougl. Ecology 52:227-239.

LEE, J.A., M.C. PRESS, S. WOODIN, AND P. FERGUSON. 1987. Responses to acidic deposition in ombrotrophic mires in the U.K. In: T.C. Hutchinson & K.M. Meema (eds.), Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems. Springer-Verlag, Berlin, pp. 549-560.

LEES, J.C. 1973. Soil aeration and sitka spruce seedling growth in peat. J. Ecol. 60:343-349.

LEUTERT, A. 1988. Mortality, foliage loss, and possum browsing in southern rata (*Metrosideros umbellata*) in Westland, New Zealand. New Zealand J. Bot. 26:7-20.

LINDSAY, J.H. 1971. Annual cycle of leaf water potential in *Picea engelmannii* and *Abies lasiocarpa* at timberline in Wyoming. Arctic and Alpine Research 3:131-138.

LOEHLE, C. 1988. Forest decline: endogenous dynamics, tree defenses, and the elimination of spurious correlation. Vegetatio 77:65-78.

MALMER, N. 1965. The southern mires. Acta Phytogeogr. Suecica 50:149-158.

MANION, P.D. 1981. Tree Disease Concepts. Prentice Hall Inc., Inglewood Cliffs, NJ.

MANKIEWICZ, P.S. 1987. The low pressure field porometer: a new, low cost technique for characterizing external

capillary water conduction in whole colonies of bryophytes and other small plants. The Bryologist 90:253-262.

MARCHAND, P.J., F.L. GOULET, AND T.C. HARRINGTON. 1986. Death by attrition: a hypothesis for wave mortality of subalpine *Abies balsamea*. Can. J. For. Res. 16:591-596.

MARGALEF, R. 1963. On certain unifying principles of ecology. The American Naturalist 97:357-375.

MATSON, P.A. AND R.D. BOONE. 1984. Natural disturbance and nitrogen mineralization: wave-form dieback of mountain hemlock in the Oregon Cascades. Ecology 65:1511-1516.

MATZNER, E. AND B. ULRICH. 1987. Results of studies on forest decline in northwest Germany. In: T.C. Hutchinson & K.M. Meema (eds.), Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems. Springer-Verlag, Berlin, pp. 25-42.

MATZNER, E., D. MURACH, AND H. FORTMANN. 1986. Soil acidity and its relationship to root growth in declining forest stands in Germany. Water, Air and Soil Pollution 31:273-282.

MCLAUGHLIN, D.L., S.N. LINZON, D.E. DIMMA, AND W.D. MCILVEEN. 1987. Sugar maple decline in Ontario. In: T.C. Hutchinson & K.M. Meema (eds.), Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems. Springer-Verlag, Berlin, pp. 101-116.

MCLAUGHLIN, S. AND O.U. BRÄKER. 1985. Methods for evaluating and predicting forest growth responses to air pollution. Experimentia 41:310-319.

MCVEAN, D.N. 1964. Woodland and scrub. In: J.H. Burnett (ed.), The Vegetation of Scotland. Oliver and Boyd, Edinburgh, pp. 144-167.

MILLINGTON, R.J. 1954. *Sphagnum* bogs of the New England plateau, New South Wales. J. Ecol. 42:328-344.

MOORE, P.D. 1968. Human influence on the vegetational history of North Cardiganshire. Nature 217:1006-

1009.

Moore, P.D. 1975. Origin of blanket mires. Nature 256:267-269.

Mueller-Dombois, D. 1983. Tree-group death in North American and Hawaiian forests: a pathological problem or a new problem for vegetation ecology? Phytocoenologia 11:117-137.

Mueller-Dombois, D. 1986. Perspectives for an etiology of stand-level dieback. Ann. Rev. Ecol. Syst. 17:221-243.

Mueller-Dombois, D. 1987. Natural dieback in forests. BioScience 37:575-583.

Mueller-Dombois, D. 1988. Forest decline and dieback – a global ecological problem. TREE 3:310-312.

Noble, M.G., D.B. Lawrence, and G.P. Streveler. 1984. *Sphagnum* invasion beneath and evergreen forest canopy in southeastern Alaska. The Bryologist 87:119-127.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164:262-270.

Palzer, C. 1983. Crown symptoms of regrowth dieback. Pac. Sci. 37:465-470.

Paratley, R.D. and T.J. Fahey. 1986. Vegetation-environment relations in a conifer swamp in central New York. Bull. Torrey Bot. Cl. 113:357-371.

Pomerleau, R. and M. Lortie. 1962. Relationships of dieback to the rooting depth of white birch. For. Sci. 8:219-224.

Potzger, J.E. 1934. A notable case of bog formation. Am. Midl. Nat. 15:567-580.

Prinz, B., G.H.M. Krause, and K.D. Jung. 1987. Development and causes of novel forest decline in Germany. In: T.C. Hutchinson & K.M. Meema (eds.), Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems. Springer-Verlag, Berlin, pp. 1-24.

RAEYMAEKERS, G. AND J.M. GLIME. 1986. Effects of simulated acidic rain and lead interaction on the phenology and chlorophyll content of *Pleurozium schreberi* (Bird.) Mitt. Journal of the Hattori Botanical Laboratory 61:425-443.

RAUP, H.M. 1963. Some problems in ecological theory and their relation to conservation. Br. Ecol. Soc. Jub. Symp. 1:19-28.

REINERS, W.A. AND G.E. LANG. 1979. Vegetation patterns and processes in the balsam fir zone, White Mountains, New Hampshire. Ecology 60:403-417.

REINERS, W.A., I.A. WORLEY, AND D.B. LAWRENCE. 1971. Plant diversity in a chronosequence at Glacier Bay, Alaska. Ecology 52:55-69.

REINIKAINEN, A., T. LINDHOLM, AND H. VASANDER. 1984. Ecological variation of mire site types in the small kettle-hole mire Heinisuo, southern Finland. Ann. Bot. Fennici 21:79-101.

RIGG, G.B. 1917. Forest succession and rate of growth in sphagnum bogs. J. For. 15:726-739.

RIGG, G.B. 1925. Some sphagnum bogs of the north Pacific coast of America. Ecology 6:260-278.

RIGG, G.B. AND P.D. STRAUSBAUGH. 1949. Some stages in the development of *Sphagnum* bogs in West Virginia. Castanea 14:129-148.

ROCHEFORT, L. 1987. Biological effects of wet acid deposition on peatland bryophytes. Masters thesis, University of Alberta, Edmonton.

ROCHEFORT, L. AND D.H. VITT. 1988. Effects of simulated acid rain on *Tomenthypnum nitens* and *Scorpidium scorpioides* in a rich fen. The Bryologist 91:121-129.

ROTH, P., C. BLANCHARD, J. HARTE, H. MICHAELS, AND M.T. EL-ASHRAY. 1985. The American west's acid rain test. World Resource Institute Research Report No. 1.

SCHULZE, E.D. 1989. Air pollution and forest decline in a spruce (*Picea abies*) forest. Science 244:776-783.

SCHÜTT, P. AND E. COWLING. 1985. Waldsterben, a general decline of forests in central Europe: symptoms,

development, and possible causes. Plant Disease 69:548-558.

SCHWINTZER, C.R. 1978. Nutrient and water levels in a small Michigan bog with high tree mortality. Am. Midl. Nat. 100:441-451.

SHAW, C.G., III, A. EGLITIS, T.H. LAURENT, AND P.E. HENNON. 1985. Decline and mortality of *Chamaecyparis nootkatensis* in southeastern Alaska, a problem of long duration but unknown cause. Plant Disease 69:13-17.

SHAW, W.B. 1983. Tropical cyclones: determinants of pattern and structure in New Zealand's indigenous forests. Pac. Sci. 37:405-414.

SHERMAN, R.J. AND R.K. WARREN. 1988. Factors in *Pinus ponderosa* and *Calocedrus decurrens* mortality in Yosemite Valley, USA. Vegetatio 77:79-85.

SHORTLE, W.C. AND K.T. SMITH. 1988. Aluminum-induced calcium deficiency syndrome in declining red spruce. Science 240:1017-1018.

SJÖRS, H. 1950. Regional Studies in north Swedish mire vegetation. Bot. Notiser 103:174-222.

SJÖRS, H. 1963. Bogs and fens on Attawapiskat River, northern Ontario. National Museum of Canada Bulletin 186:45-133.

SKENE, M. 1915. The acidity of *Sphagnum*, and its relation to chalk and mineral salts. Ann. Bot. Lond. 29:65-87.

SKIPWORTH, J.P. 1983. Canopy dieback in a New Zealand mountain beech forest. Pac. Sci. 37:391-395.

SLATYER, R.O. 1976. Water deficits in timberline trees in the Snowy Mountains of south-eastern Australia. Oecologia 24:357-366.

SMITH, J.M.B. AND L.F. KLINGER. 1985. Aboveground:belowground phytomass ratios in Venezuelan páramo vegetation and their significance. Arct. Alp. Res. 17:189-197.

SOIL SURVEY STAFF. 1975. Soil Taxonomy. USDA Soil Conservation Service Agriculture Handbook No. 436.

SOKAL, R.R. AND F.J. ROHLF. 1981. Biometry. W.H. Freeman and Company, San Francisco.

SPAULDING, P. AND H.J. MACALONEY. 1931. A study of organic factors concerned in the decadence of birch in cutover lands in northern New England. Journal of Forestry 29:1134-1149.

SPRAGUE, R. AND D.B. LAWRENCE. 1960. The fungi of deglaciated Alaskan terrain of known age. Wash. State Univ. Res. Stud. 28:1-20.

SPRUGEL, D.G. 1976. Dynamic structure of wave-generated Abies balsamea forests in the northeastern United States. J. Ecol. 64:889-911.

STALEY, J.M. 1965. Decline and mortality of red scarlet oaks. For. Sci. 11:2-17.

STEPHENSON, S.L. AND H.S. ADAMS. 1986. An ecological study of balsam fir communities in West Virginia. Bull. Torrey Bot. Cl. 113:372-381.

STEWART, G.H. AND T.T. VEBLEN. 1982. Regeneration patterns in southern rata (*Metrosideros umbellata*) - kamahi (*Weinmannia racemosa*) forest in central Westland, New Zealand. New Zealand J. Bot. 20:55-72.

TAMM, C.O. 1976. Acid precipitation: biological effects on soil and on forest. Ambio 5:235-238.

TOOLE, E.R. AND W.M. BROADFOOT. 1959. Sweetgum blight as related to alluvial soils of the Mississippi River floodplain. For. Sci. 5:2-9.

TVEITE, B. 1987. Air pollution and forest damage in Norway. In: T.C. Hutchinson & K.M. Meema (eds.), Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems. Springer-Verlag, Berlin, pp. 59-67.

TYLER, G., D. BERGGREN, B. BERGKVIST, U. FALKENGREN-GRERUP, L. FOLKESON, AND A. RUHLING. 1987. Soil acidification and metal solubility in forests of southern Sweden. In: T.C. Hutchinson & K.M. Meema (eds.), Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems. Springer-Verlag, Berlin, pp. 347-359.

TYREE, M.T. AND J.S. SPERRY. 1988. Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Plant Physiol. 88:574-580.

TYREE, M.T., L.B. FLANAGAN, AND N. ADAMSON. 1987. Response of trees to drought. In: T.C. Hutchison and K.M. Meema (eds.), Effects of Atmospheric Pollutants on Forests, Wetlands and Agricultural Ecosystems. Springer-Verlag, Berlin, pp. 201–216.

ULRICH, B., R. MAYER, AND P.K. KHANNA. 1980. Chemical changes due to acid precipitation in a loess-derived soil in central Europe. Soil Science 130:193-199.

UGOLINI, F.C. AND D.H. MANN. 1979. Biopedological origin of peatlands in southeast Alaska. Nature 281:366-368.

VEBLEN, T.T. , D.H. ASHTON, F.M. SCHLEGEL, AND A.T. VEBLEN. 1977. Distribution and dominance of species in the understory of a mixed evergreen-deciduous Nothofagus forest in south-central Chile. J. Ecol. 65:815-830.

VEBLEN, T.T. AND D.H. ASHTON. 1982. The regeneration status of *Fitzroya cupressoides* in the Cordillera Pelada, Chile. Biol. Conserv. 23:141-161.

VEBLEN, T.T. AND D.C. LORENZ. 1987. Post-fire stand development of Austrocedrus – Nothofagus forests in northern Patagonia. Vegetatio 71:113-126.

VEBLEN, T.T. AND D.C. LORENZ. 1988. Recent vegetation changes along the forest/steppe ecotone of northern Patagonia. Annals of the Association of American Geographers 78:93-111.

VEBLEN, T.T. AND G.H. STEWART. 1982. On the conifer regeneration gap in New Zealand: the dynamics of *Libocedrus bidwillii* stands on South Island. J. Ecol. 70:413-436.

VIERECK, L.A. 1966. Plant succession and soil development on gravel outwash of the Muldrow Glacier, Alaska. Ecological Monographs 36:181-199.

VIERECK, L.A. 1970. Forest succession and soil development adjacent to the Chena River in interior Alaska. Arct. Alp. Res. 2:1-26.

VOGELMANN, H.W., G.J. BADGER, M. BLISS, AND R.M. KLEIN. 1985. Forest decline on Camels Hump, Vermont. Bull. Torrey Bot. Cl. 112:274-287.

WALKER, D. 1970. Direction and rate in some British post-glacial hydroseres. In: D. Walker & R.G. West (eds.), Studies in the Vegetational History of the British Isles. Cambridge University Press, London, pp. 117-139.

WALKER J., C.H. THOMPSON, AND W. JEHNE. 1983. Soil weathering stage, vegetation succession, and canopy dieback. Pac. Sci. 37:471-481.

WARD, L.K. 1982. The conservation of juniper: longevity and old age. J. Appl. Ecol. 19:917-928.

WARDLE, J.A. AND R.B. ALLEN. 1983. Dieback in New Zealand Nothofagus forests. Pac. Sci. 37:397-404.

WARDLE, P. 1980. Primary succession in Westland National Park and its vicinity, New Zealand. New Zealand J. Bot. 18:221-232.

WATERMAN, W.G. 1926. Ecological problems from the sphagnum bogs of Illinois. Ecology 7:255-272.

WEBER, C.A. 1908. Aufbau und Vegetation der Moore Norddeutschlands. Engler's Bot. Jahrb. 40(Suppl.):19-34.

WESTING, A.H. 1966. Sugar maple decline: an evaluation. Econ. Bot. 20:196-212.

WILE, I., G.E. MILLER, G.G. HITCHIN, AND N.D. YAN. 1985. Species composition and biomass of the macrophyte vegetation of one acidified and two acid-sensitive lakes in Ontario. Can. Field-Naturalist 99:308-312.

WOODMAN, J.N. 1987. Pollution-induced injury in North American forests: facts and suspicions. Tree Physiology 3:1-15.

ZACH, L.W. 1950. A northern climax, forest or muskeg? Ecology 31:304-306.

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